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PALAEONTOLOGY

VOLUME 1 · PART 1

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THE TRUE *RHYNCHONELLA*

by D. V. AGER

ABSTRACT. The well-known brachiopod genus *Rhynchonella* was erected by Fischer de Waldheim in 1809. It was founded on a new species *R. loxia* from the Upper Jurassic of the Moscow region. On the basis of topotype material, this species is here revised and redescribed with details of internal structures not previously studied. Other species which may belong to *Rhynchonella* s.s. are also discussed.

INTRODUCTION

A DISTINGUISHED palaeontologist recently commented in a discussion: 'There is a real need for palaeontology to return to the habit of calling a spade a spade and a *Rhynchonella* a *Rhynchonella*.' The present author agrees with the general sentiment of this remark, but not with the particular palaeontological example. It is the customary complaint of the specialist in one field of palaeontology that the genera in other fields are too finely subdivided. Let us, by all means, be content to call a rhynchonellid a rhynchonellid, but a generic name of the scope of *Rhynchonella sensu lato* no longer has any real value. In the widest sense, as generally recognized by non-specialists, it is a vast 'dust-bin' genus ranging from Ordovician to Holocene in age and including several thousand species. More than 150 genera have been defined within this group, and even though many of these may not be acceptable, there are certainly many more undescribed. The group as a whole is now variously regarded as a superfamily, a suborder, or even an order. This at least gives an indication of the complexity of the group, which is only obscured by 'lumping'. In view of the time-range and the number of species involved, to call all these forms by the one name '*Rhynchonella*' is even less desirable than to call all the Mesozoic ammonoids by the one name '*Ammonites*'.

A genus is, of course, merely a convenient fiction. Such fictions in the rhynchonelloids are valuable in that they enable us to distinguish the numerous lines of species that evolved, side by side, from the Ordovician onwards. Among the Mesozoic rhynchonellids, it is impossible to make any progress towards understanding the complex pattern of evolution within the group, until many of the vast number of described species are grouped together. The use of Buckman's often-derided generic names for brachiopods is not therefore so much a matter of futile 'splitting' as of useful 'lumping'. For all these reasons, it is considered highly desirable to place on record exactly what was meant by *Rhynchonella* when the name was first proposed.

Special note. Throughout this paper Russian place-names (apart from Moscow) are spelt according to the modern rules of transliteration now accepted in both Great Britain and the U.S.A. Many variants of these spellings are to be found in the literature and on museum labels.

[Palaeontology, Vol. 1, Part 1, 1957, pp. 1–15, pls. 1–2]

SYSTEMATIC PALAEONTOLOGY

Suborder RHYNCHONELLOIDEA Moore 1952
Superfamily RHYNCHONELLACEA Schuchert 1896
Family RHYNCHONELLIDAE Gray 1848
Subfamily RHYNCHONELLINAE Gill 1871

Genus RHYNCHONELLA Fischer 1809

Rhynchonella Fischer 1809, p. 35.
Rhynchonellis Fischer, Keferstein 1829, p. 50.
Rhyngonella Fischer 1843, p. 117.
Rhynchonella Fischer, Rouillier and Vossinsky 1847, p. 394.
Rhynchonella Fischer, Hall and Clarke 1894, p. 823.
Rhynchonella Fischer, Buckman 1918, p. 57.
Eurhynchonella Leidhold 1920, p. 352.
Rhynchonella Fischer, Wisniewska 1932, p. 13.
Rhynchonella Fischer, Gerasimov 1955, p. 217.

Type species (by original definition). *Rhynchonella loxia* Fischer.

Emended diagnosis. Small to medium-sized, everted rhynchonellids. Subtrigonal in outline, gibbous or convexi-planate and cynocephalous in lateral view. Subcircular, depressed and biconvex in neanic stage. Usually a high fold in dorsal valve, and strong, sharp uniplication in anterior commissure. Both valves smooth posteriorly, costae few and sharp, developing late. Fine radial striae on well-preserved specimens. Beak small, slightly incurved, hypothyrid to submesothyrid. Strong dental plates. No cardinal process. Shallow septalium between hinge-plates and short dorsal median septum. Crura short, radulifer type.

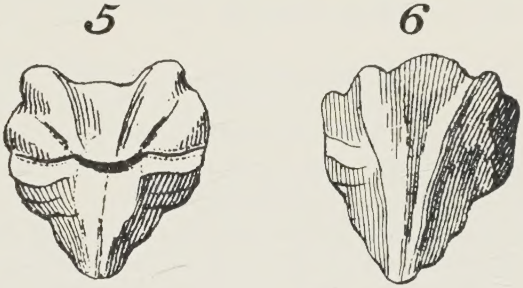
Discussion. Since *R. loxia* is almost the only species which can be attributed to *Rhynchonella* s.s. with any certainty, a generic description cannot be separated from that of the type species. Similarly, the generic diagnosis given above may require amendment if further species are confirmed.

Fischer de Waldheim (1809, p. 35) first proposed the name *Rhynchonella* in the course of describing some Jurassic fossils collected near Moscow. He distinguished the 'Rhynchonelles' as 'Térébratules à lobes intermédiaires si allongés qu'il en résulte la forme d'un bec. La pointe du bec est avec le trou du sommet dans le même plan.' He went on to define his new genus by the following characters, most of which are found in the majority of brachiopods: 'Coquille bivalve, régulière, à valves inégales, se fixant par un ligament ou un tube court; la plus petite valve perforée a son sommet peu proéminent, non recourbé; charnière à . . . dents.'

He clearly regarded his new species '*R. Loxiae*' (see text-fig. 1) as exemplifying his new genus. Fischer referred to *Rhynchonella* again in later publications (1825, 1830, 1837). In the last of these, however, he rejected what he then called his 'sous-genre de Térébratule' and reverted to Schlotheim's ubiquitous name '*Terebratula variabilis*' for his type species.

Keferstein gave '*Rhynchonellis*' as a genus in his catalogue (1829), apparently as a misreading of the Gallicized 'Rhynchonelles' in Fischer's later paper (1825, p. 6).

Later still Fischer (1843) changed his mind again and referred his Moscow form (which he misspelt '*Rhyngonella*') to Sowerby's species *Terebratula acuta.* This was followed by a long series of papers by Rouillier (1844, 1846, 1849) and Rouillier and Vossinsky (1847–8) in which the variations of Fischer's species and its relations were examined at length. In the last of these, the genus *Rhynchonella* may be said to have been discussed for the first time, and compared with *Terebratula.*



TEXT-FIG. 1. *Rhynchonella loxia* Fischer. Upper Jurassic, Tatarovop, near Moscow. Reproduction of original figures published by Fischer de Waldheim (1809, pl. 2, figs. 5, 6). 5 is the posterior view, 6 the anterior view, the ventral valve is uppermost in both cases, × 2 approximately.

The name *Rhynchonella* only crept into the non-Russian literature very slowly. It did not reach the French literature until it was accepted by d'Orbigny in 1847. It was brought to the notice of British palaeontologists by Davidson (1852, p. 65 and elsewhere) who provided a translation of Fischer's original remarks. The great German workers of the last century continued to use the name *Terebratula* for the rhynchonellids, though Quenstedt did use '*Rhynchonella*' for a few American Palaeozoic forms (1885, pl. 54) whilst curiously retaining *Terebratula* for a topotype specimen of Fischer's type species (ibid., pl. 53, fig. 54).

Rothpletz (1886) appears to have been the first to realize the need for finer definition within the great concourse of species that had gathered around the generic name *Rhynchonella.* He proposed thirty-five divisions which would be genera in the modern sense, though he did not give them generic names. Similarly, Buckman and Walker (1889) proposed eight groups among the Jurassic rhynchonellids and suggested the desirability of erecting a number of new genera or subgenera.

The first useful redefinition of *Rhynchonella* s.s. was made by Hall and Clark (1894, p. 823), who recognized the need '. . . for closer discriminations in this great group of species . . .'. Buckman, in his 'Burma Memoir' (1918), erected most of the Jurassic rhynchonellid genera now in use and redefined *Rhynchonella* s.s. in his own distinctive way (op. cit., p. 57), excluding from it practically all the forms that had previously been included.

Leidhold (1920) independently expressed the need for some grouping of the many rhynchonellid species, but he concentrated on different characters from those used by Buckman. He favoured the retention of the name *Rhynchonella* in a general sense only, and proposed the name *Eurhynchonella* for the acutely-folded forms typified by *R. loxia*. This, however, is quite unacceptable under the rules of nomenclature.

Wisniewska (1932, p. 13) revised the genus with the aid of topotype specimens of *R. loxia* and gave details of various internal structures not previously described. This is the most valuable account of *Rhynchonella* s.s. at present available. Recently, Gerasimov (1955, pp. 218 et seq.), in reviewing the Mesozoic fossils of the Moscow region, recognized *Rhynchonella* in its modern restricted sense. He redescribed it briefly and figured a topotype specimen of the type species.

Rhynchonella loxia Fischer

Plates 1 and 2; text-figs. 1–4

Rhynchonella Loxiae Fischer 1809, p. 35, pl. 2, figs. 5, 6.
Rhynchonella Loxiae Fischer 1830, pl. 23, figs. 8*a*, *b*.
Terebratula variabilis Schlotheim, Fischer 1837, p. 147, pl. 23, figs. 8*a*, *b*.
Terebratula acuta Sowerby, Fischer 1843, p. 117.
Terebratula aptycha Fischer 1843, p. 124, pl. 4, figs. 7–9.
Terebratula acuta Sowerby, Rouillier 1844, p. 889, pl. 22, figs. 1–10.
Terebratula aptycha Fischer, d'Orbigny *in* Murchison *et al.* 1845, p. 482, pl. 42, figs. 22–26.
Terebratula Loxiae Fischer, Rouillier 1846, p. 441.
Terebratula acuta Sowerby, Rouillier and Vossinsky 1847–8, p. 375, pl. F, figs. 2, 3.
Rhynchonella Loxiae Fischer, Eichwald 1866, p. 320.
Terebratula acuta Sowerby, Quenstedt 1885, p. 693, pl. 53, fig. 54.
Rhynchonella loxia Fischer, Hall and Clarke 1894, p. 822, pl. 42, figs. 1–3.
Rhynchonella loxia Fischer, Buckman 1918, p. 57, pl. 18, figs. 30, 31.
Rhynchonella Loxiae Fischer, Lewinski 1923, p. 45, pl. 8, figs. 3*a*–*d*.
Rhynchonella loxia Fischer, Wisniewska 1932, p. 14, pl. 6, figs. 19, 20.
Rhynchonella loxiae Fischer, Gerasimov 1955, p. 219, pl. 43, figs. 8, 9.

Emended diagnosis. Small *Rhynchonella* up to about 17 mm. long, 18 mm. wide, and 16 mm. thick. Trigonal in outline, ventral valve flat. High, sharp uniplication and fold, characteristically containing only one costa. Ventral sinus deep, somewhat U-shaped, often with median groove. Usually two costae on either side of fold. Beak small, slightly incurved.

Type specimen. Professor A. N. Sokolskaya has informed the author that Fischer's type specimen is lost (personal communication, January 1956). It was presumably destroyed with the rest of Fischer's collection in the great fire of 1812 when Moscow was occupied by the army of Napoleon Buonaparte (*vide* Fischer 1830, p. viii). It is not considered desirable to propose a neotype for a species of foreign origin and authorship, and although the species is of great importance, there has never been any confusion over its identity.

Material and distribution. Only a limited number of specimens of *Rhynchonella loxia* are available in Britain. Fischer originally recorded the species from Tatarovo, on the south bank of Moscow River about 10½ km. west-north-west of the Russian capital. The sections here were described in English by Murchison, Verneuil, and Keyserling (1845). No specimens are known to the author from Tatarovo; the vast majority of those mentioned in literature and available in collections are from Khoroshevo on the opposite bank of the river. From the geological map and from stratigraphical accounts such as that mentioned above, it would appear that the uppermost Jurassic rocks are restricted to this side of the river.

There are a number of Russian examples of *Rhynchonella loxia* in the British Museum (Natural History) and a few in the Geological Survey Museum and in the Sedgwick Museum at Cambridge. Almost all of these which have detailed labels come from Khoroshevo. This is also the locality mentioned by Gerasimov (1955, p. 219) and is the origin of a number of specimens which he very kindly gave to the present author. A few specimens in the British Museum (Natural History) came from Mnevniki, about 2 km. farther south.

The age of the deposit concerned is variously recorded on British Museum labels as 'Oxfordian', 'Kimeridgian', and 'Portlandian'. According to Gerasimov (loc. cit.) it belongs to the J_3vlg.s.ct division in the Russian nomenclature, i.e. the zone of *Craspedites subditus*. He also recorded *R. loxia* from other localities in the Moscow region at higher and lower horizons (the zones of *Craspedites nodiger* and *Kachpurites fulgens* respectively). These three zones form the upper part of the Volgian, that is the post-Middle Kimeridgian Jurassic, which cannot be correlated accurately with the west European successions (Arkell 1956, p. 8).

Lewinski (1923) described and figured *R. loxia* from the 'Bononian' (i.e. Volgian) of Brzostowka in Poland. Wisniewska (1932, p. 16) noted that this species is very rare in the Polish Upper Jurassic and only occurs in the Volgian in the vicinity of Tomaszów. Rozycki (1948) listed this species from the 'Bononian' in his valuable paper on the Upper Jurassic rhynchonellids of the Cracow–Czestochowa chain in Poland, but he did not discuss it otherwise, and it would not appear therefore to be a very important member of the fauna. The present author does not know of any records of this species from elsewhere.

Description. External characters. R. loxia is a small to medium-sized rhynchonellid. Specimens examined by the author showed the following range in dimensions:

	Minimum (*mm.*)	*Mode* (*mm.*)	*Maximum* (*mm.*)
Length	8·0	10·1–10·5	13·8
Width	8·6	12·1–12·5	16·8
Thickness . . .	6·6	11·6–12·0	15·5

In its earliest growth-stages, the shell is biconvex, depressed and circular in outline, like most Mesozoic rhynchonellids. With growth, the dorsal valve continues to be convex, whilst the ventral becomes almost flat. In the adult, the shell is subtrigonal in outline with rounded antero-lateral angles. The apical angle ranges from about 85° to about 115°, but is usually close to 100°. The valves meet anteriorly at a fairly obtuse angle, and some large specimens show a sudden decrease in growth-rate shortly before the cessation of growth (e.g. Sedgwick Museum specimen F. 9. 678).

The most distinctive features of the shell are the very sharp uniplication in the anterior commissure, and the very strong, sharp dorsal fold which begins to develop when the shell reaches about one-third of its ultimate size. The linguiform extension is correspondingly long and sharply trigonal, but the sinus is curiously shallow, having a flat floor usually with a central groove anteriorly. This contrasts markedly with the deep, sharp sinus of *Homoeorhynchia acuta* (J. Sowerby) which was recently redescribed by the present author (Ager 1956, p. 20) and which otherwise closely resembles the present species in shape. Occasional specimens show the sharp uniplication without a correspondingly strong fold (see Pl. 1, figs. 2*b*, *c*). This appears to have resulted from the early cessation of shell-growth in the middle of the dorsal valve, so that the linguiform extension is folded back to fill the resultant embayment. Such specimens may be merely pathological oddities.

In lateral view the shell is usually trigonal in outline. The line from the beak along the crest of the fold makes an angle with the lateral commissure which ranges from about 45° to more than 90°; in the majority it is between 60° and 80°. The variations in all the above external characters were well described and figured by Rouillier (1844), when dealing with what were almost certainly topotype specimens of this species. It would be most unwise to attempt a variation study here without the benefit of personally collected material.

There is normally only a single costa on the crest of the fold, the sides of which are smooth. One specimen examined in the course of this study (Sedgwick Museum specimen F. 9. 797) has a second costa faintly developed in the fold. This may be transitional to the bi- and tri-costate forms discussed below. There are almost invariably two costae on either side of the fold, though traces of a third can also sometimes be observed. These costae are fairly sharp (the *tetrahedra* type of Ager 1956, p. viii) and appear just after the fold. Faint growth-lines are often visible.

In well-preserved specimens, both valves bear faint radial striae extending from the beak to the anterior margin (see Pl. 1, fig. 3*b*). Buckman (1918) placed considerable emphasis on this character, which he referred to as capillation. The faint lines seen on *R. loxia*, however, appear not to be true capillae, but merely an effect produced in slightly worn specimens due to the exceptionally fibrous nature of the shell. The lines are seen at all levels in the shell, but are less marked when it is relatively unworn. The calcite fibres lie at a very oblique angle and the shell readily flakes away. Since almost all of the specimens seen come from a single locality—Khoroshevo—it is possible (but not likely) that the above character is merely a secondary feature of local preservation. The same fine striae were observed in specimens of *R. rouillieri* (see below) from the nearby Lower Volgian locality of Mnevniki. It is probable that this character, and others discussed

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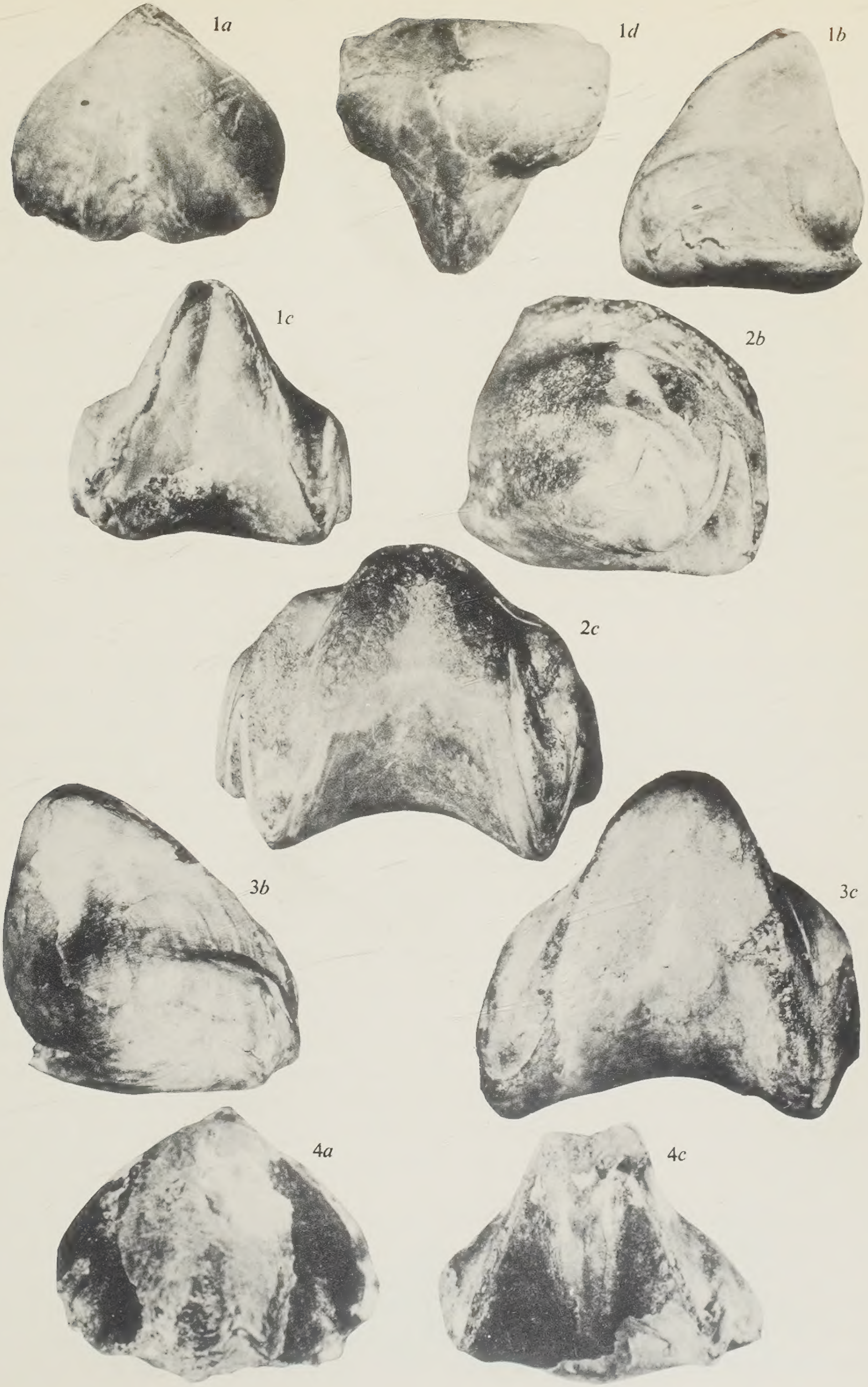
EXPLANATION OF PLATE 1

In each case (*a*) is the dorsal view, (*b*) the lateral view, (*c*) the anterior view, and (*d*) the posterior view. BM = British Museum (Natural History), London; SM = Sedgwick Museum, Cambridge.

Figs. 1–3. *Rhynchonella loxia* Fischer. 1*a–d*, BM BB. 17578, ×3. Zone of *Craspedites subditus*, Upper Volgian, Khoroshevo, near Moscow. Well-preserved specimen showing the typical appearance of the species. Gerasimov collection presented by the author to the British Museum (Natural History). 2*b*, *c*, SM F. 9. 801, ×4. Labelled 'Oxford Clay'—probably Upper Volgian—Khoroshevo, near Moscow. An unusual form in which the uniplication is strongly developed but there is scarcely any dorsal fold. As a result there is a deep embayment in the dorsal valve, the lateral parts of which are half as long again as the centre part. 3*b*, *c*, SM F. 9. 674, ×4½. Labelled 'Portlandian'—probably Upper Volgian—Khoroshevo, near Moscow. A large well-preserved specimen in which the fold is developed to an exceptional degree. The fine radial striae or 'capillae' are clearly visible.

Figs. 4*a*, *c*. *Rhynchonella rouillieri* Eichwald. BM B. 2183, ×3. Labelled 'Kimmeridgian'—probably Lower Volgian—Mnevniki, near Moscow. An example of what is probably a closely related species with bi-costate fold, more upright beak and more depressed lateral profile.



AGER, *Rhynchonella*

below, are seen because of the exceptionally good preservation of fossils in this neighbourhood, which often have the opalescent outer nacreous layer intact. This has been noted by several authors, including Fischer (1809, p. 35), Murchison *et al.* (1845, p. 236), and Arkell (1956, p. 492).

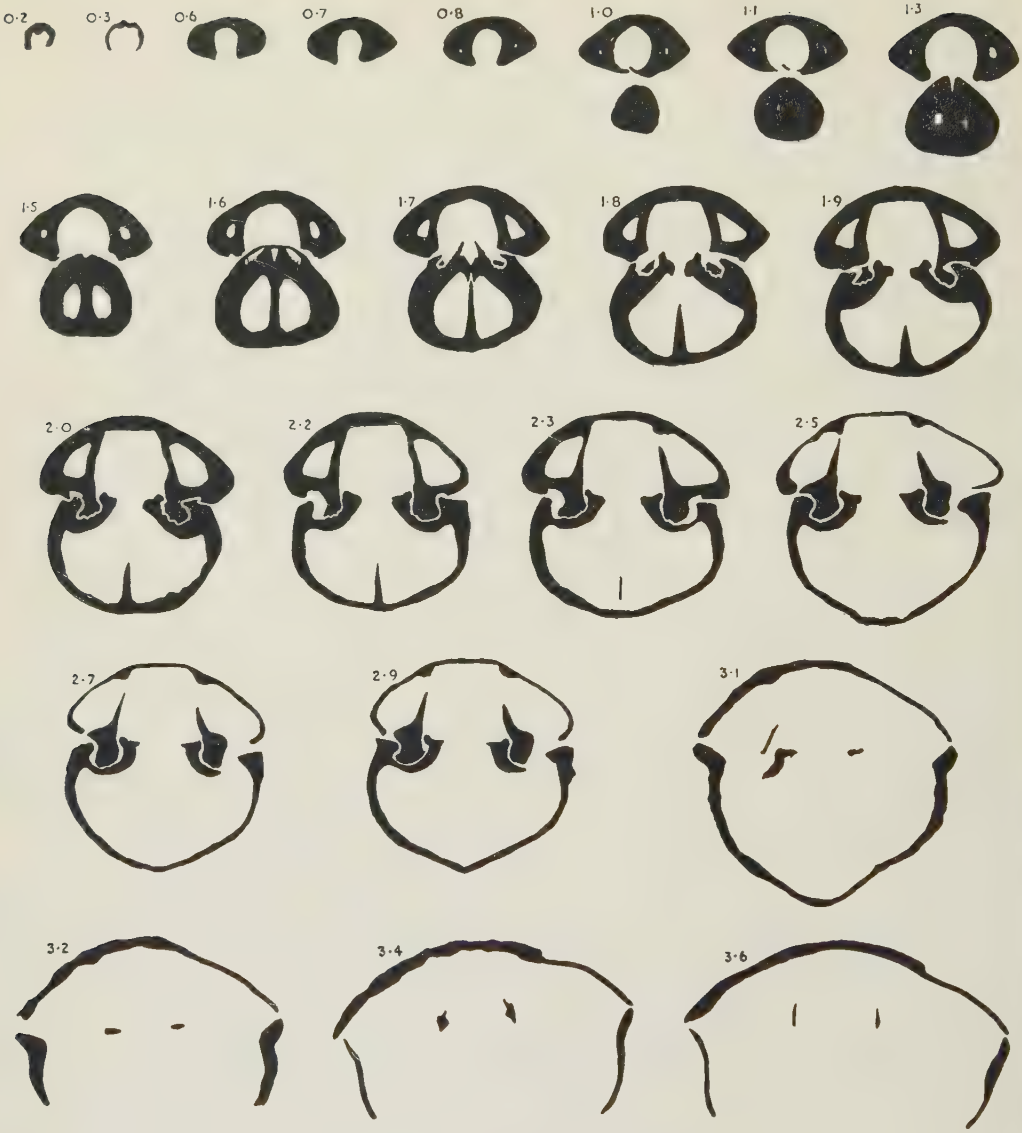
The beak is small and slightly incurved, with faint beak-ridges delimiting a wide, low interarea. The pedicle-opening is small, circular to elliptical and hypothyrid to submesothyrid. The deltidial plates are narrow, trigonal, and just conjunct.

Internal characters. Before describing the internal characters of the separate valves, it is necessary to mention a shell feature which is observable on the inner surface of both valves and on internal moulds. This is a *Schuppenpanzerstruktur* or 'shell-mosaic' produced by the proximal ends of the calcite fibres forming the shell wall (see Pl. 2, fig. 1). This was first described by Blochmann (1908) in three living rhynchonellid species; he did not think that it would preserve in fossils. Leidhold (1920) found it in a few Jurassic rhynchonellids from Germany. He argued that this character—in its various forms—was potentially of very great importance in the classification of fossil rhynchonellids. It therefore seems desirable to place on record the form of the scales in the type species of *Rhynchonella*. The 'scales' appear to be arranged in a somewhat haphazard pattern, but are constant in shape. Their outlines are much more pointed distally than in any of those figured by Blochmann (op. cit., pl. 37) and Leidhold (op. cit., pl. 4). It is doubtful if this character will ever be of any practical value in unravelling relationships, as it is only preserved in exceptional circumstances.

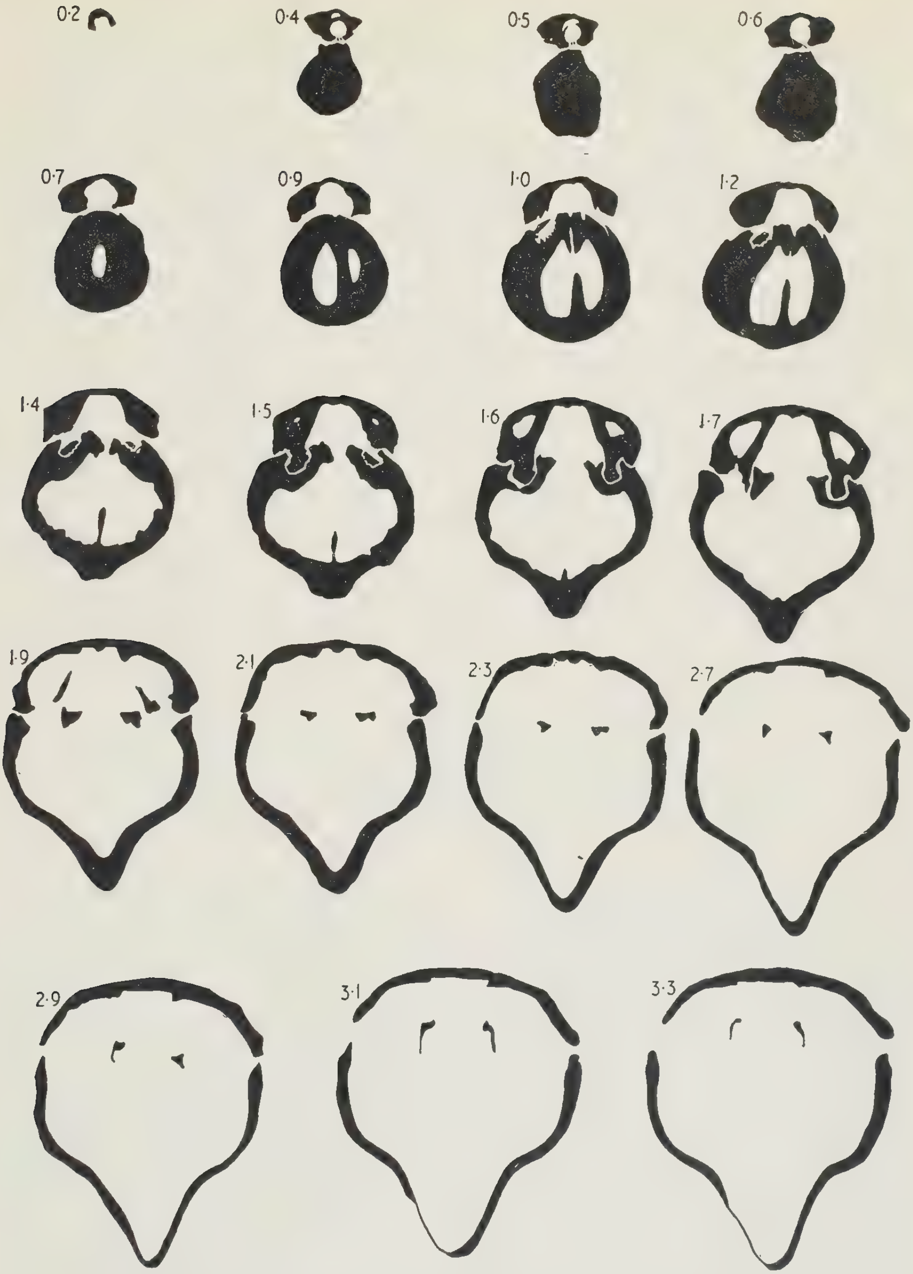
Owing to the limited number of specimens available in Britain, it was not possible to section many to study internal structures. Two specimens were ground following the techniques developed by Dr. H. M. Muir-Wood, and recently summarized by the present author (Ager 1956, p. iii). These are shown in text-figs. 2 and 3. Cellulose peels and photographs were taken of the sections as they were exposed, to act as a permanent record. It was also possible, through the kindness of Dr. Muir-Wood, to study a set of sections made under her direction at the British Museum (Natural History).

Ventral valve. A small pedicle-collar was observed in one specimen (see text-fig. 3). There are strong dental plates which diverge slightly both dorsally and anteriorly. Their forward edges are slightly inclined, so that in transverse sections they are seen to break away at, or just beyond, the plane of articulation (as defined by Ager, op. cit., p. vii). The dental plates directly support strong, crenulated teeth. Short, blunt denticula are developed laterally. No septa or ridges have been observed in the ventral valve. The ventral muscle-scars are usually difficult to observe. The diductor muscle-scars form a somewhat elongated oval area, extending about one-third of the length of the valve in adult specimens. They completely surround the rather small impressions of the adductor muscles (see text-fig. 4). Small adjustor muscle impressions are sometimes visible laterally, and the muscle area as a whole is often surrounded laterally and posteriorly by ovarian impressions.

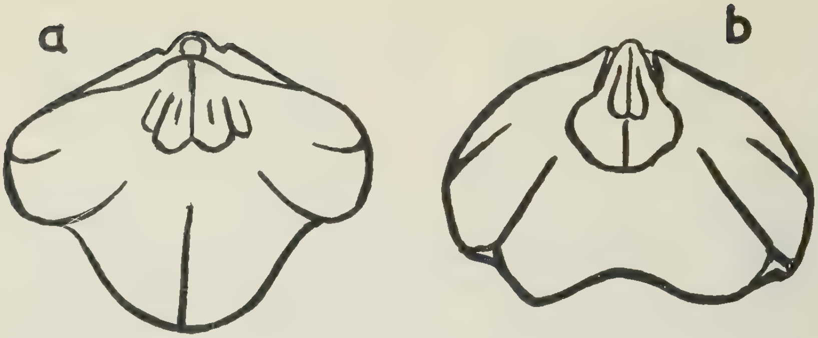
Dorsal valve. There is no cardinal process. The stout median septum breaks away from the septalial plates at an early stage and does not extend beyond the plane of articulation. A shallow septalium is developed between short hinge-plates. Both inner and outer socket-ridges are short, blunt, and fairly clearly demarcated. The main sockets are deep and crenulated; the accessory sockets are shallow and poorly defined. There are no distinct crural bases. The crura are of the radulifer type, short and flattened in the



TEXT-FIG. 2. Camera lucida drawings of twenty-three transverse sections through the posterior part of a specimen of *Rhynchonella loxia* Fischer from the Upper Volgian of Khoroshevo, near Moscow. The top three rows show the form of the delthyrial and umbonal cavities in the ventral valve and the nature of the articulation. The bottom two rows show the form of the crura. The last three sections show part only of the dorsal valve. It is possible that much of the umbonal cavities and part of the delthyrial cavity may be filled anteriorly with secondary calcite or callus. Original length of the specimen 10·5 mm. The small figures refer to the distances in millimetres from the anterior point at which grinding was commenced. The crura finally disappeared at 3·8 mm. from this point. BM (B. 1325). All $\times 4\frac{2}{3}$ approximately.



TEXT-FIG. 3. *Rhynchonella loxia* Fischer. Upper Volgian, Khoroshevo, near Moscow. A confirmatory set of transverse sections, comparable to those seen in text-fig. 2 but with some additional features. The pedicle-collar and deltidial plates are seen in the second, third, and fourth sections; the seventh and eighth sections show the form of the crura, which are distally expanded and which finally disappeared at 3·6 mm. from the posterior end. Author's collection J. 1067/1, presented by Dr. P. A. Gerasimov. All ×4⅔ approximately.



TEXT-FIG. 4. *Rhynchonella loxia* Fischer. Camera lucida drawings of an internal mould from the Upper Volgian, near Moscow, showing the arrangement of the muscle-scars. (*a*) dorsal valve, (*b*) ventral valve. Specimen in the Geological Survey Museum (register number FOR. 454), figured by Buckman (1918, pl. 18, fig. 30), ×3 approximately.

dorso-ventral plane; they curve sharply towards the ventral valve and are expanded distally. The dorsal muscle-scars take the form of narrow parallelograms set well forward. The anterior adductor scars are larger than the others and are placed on either side of the end of the median septum. Ovarian impressions are sometimes seen around the muscle area.

Discussion. Fischer's original description of this species (1809, p. 35) reads as follows:

> *Rhynchonella Loxiae*, mihi; valva major bidentata, margine terminali incurvo. . . . L'espèce de Tataroba que je décris, et qui a encore tout son nacre de perle, est petite, mais très distincte. Elle a 5 lignes de hauteur, et son bec courbé presque 7 lignes de largeur. Elle est bombée à côté du sommet, de sorte qu'elle représente parfaitement bien la tête d'un oiseau.

Fischer's original figures are reproduced in text-fig. 1. For the last sixty years the specific name has usually been spelt '*loxia*'. There is no indication in Fischer's papers of the origin of the name, unless it be intended to refer to the unusual beak of a genus of finches which includes the Crossbill (*Loxia curvirostra curvirostra* Linnaeus). Without any definite suggestion of a feminine attribution, the masculine ending is to be preferred, so the modern usage is adopted here.

The transverse sections published by Wisniewska (op. cit., fig. 3) look very different from those shown in text-figs. 2 and 3. This is because they appear to have been taken at right angles to the maximum length of the shell (i.e. the line from the beak to the highest point of the fold). The resultant plane is likely to be as much as 45° different from that shown here, and the effect is to give the appearance of a very small dorsal valve and low median septum, besides altering the shape of other structures. The present author has

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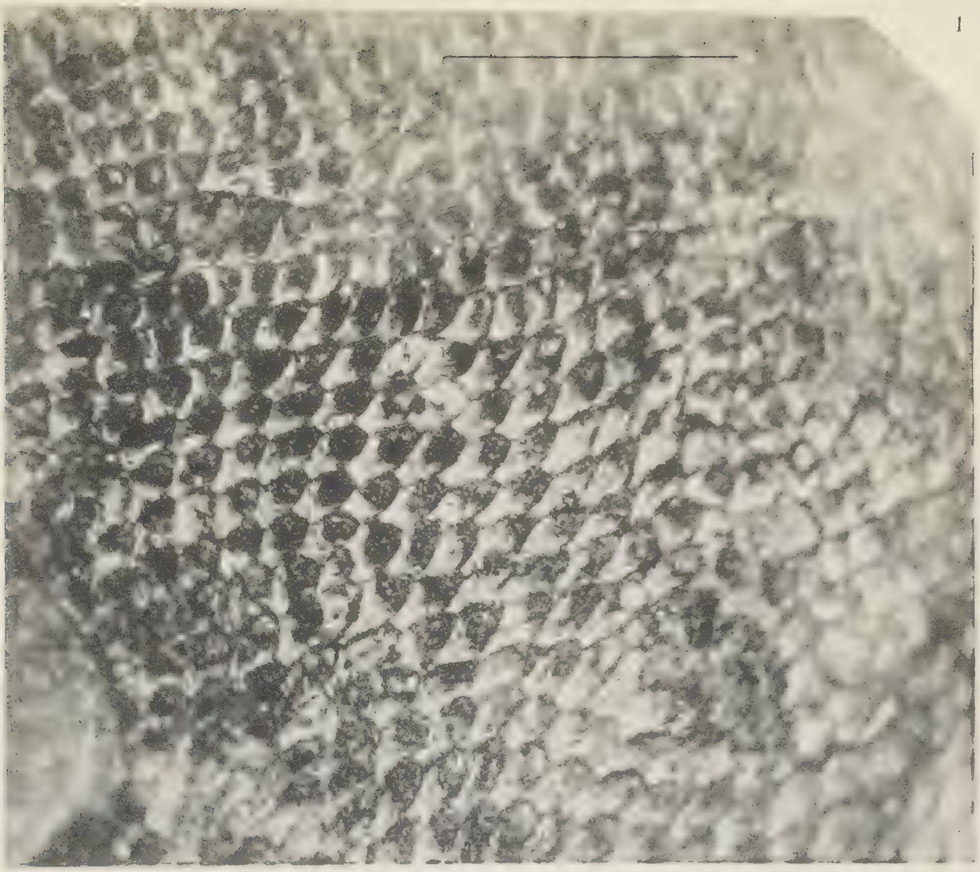
EXPLANATION OF PLATE 2

Figs. 1–3. *Rhynchonella loxia* Fischer. 1, BM, BB. 17579. Zone of *Craspedites subditus,* Upper Volgian, Khoroshevo, near Moscow. *Schuppenpanzerstruktur* or 'shell-mosaic' on inner surface of dorsal valve near the hinge-line, showing the form of the scales. The black line at the top represents one-tenth of a millimetre. 2, BM B. 1325, ×*c.* 14½. Labelled 'Oxfordian?'—probably Upper Volgian—Khoroshevo, near Moscow. Cellulose peel of a ground specimen, 1·5 mm. from the posterior end showing the microscopic structure of the shell. 3, as fig. 2, but 1·6 mm. from the posterior end, showing the development of the septalium and sockets in the dorsal valve.



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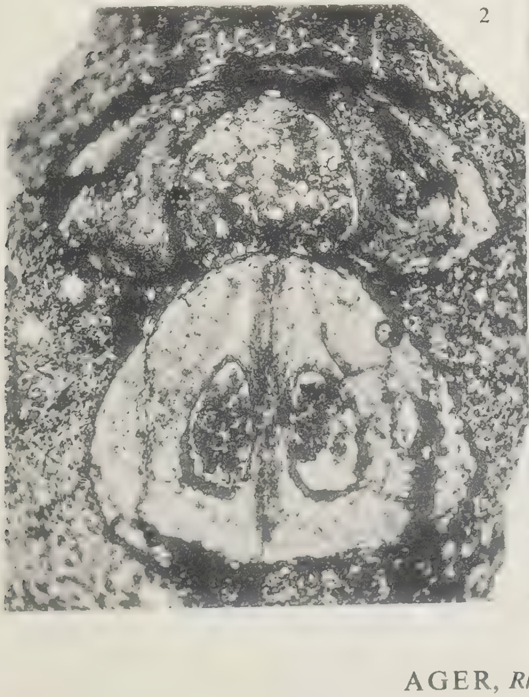

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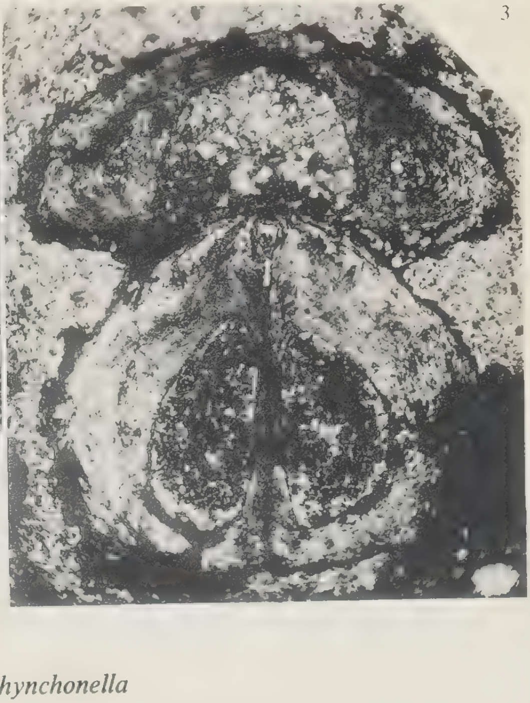

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AGER, *Rhynchonella*

discussed elsewhere (Ager 1956, p. iv) his reasons for preferring the orientation used here. It should be remembered that Wisniewska's paper was published before Dr. H. M. Muir-Wood introduced the serial grinding technique to British Mesozoic brachiopod literature.

It is not possible to discuss in detail the relationships of this species to other members of the genus *Rhynchonella* s.s., since the majority of the latter are quite unknown in Britain. The distinctiveness of *R. loxia* would seem to lie particularly in its sharp, unicostate fold.

In general it may be said that *R. loxia* is unusual, but by no means unique, in its external appearance. In this it is perhaps somewhat unfortunate as the type species of a major group of brachiopods. Internally, however, it is very much the 'average' rhynchonellid. It is probably close to the main stock of rhynchonellids which persisted from the Silurian to the present day with very little change in the essentials of their shell structure. These are all impunctate, everted forms with short, radulifer-type crura and divided hinge-plates separated by a septalium (or cruralium) which is supported by a short median septum. There is no cardinal process and no median septum in the ventral valve. Such forms may be regarded as belonging to the subfamily Rhynchonellinae. Other forms, with features such as inverted shells (e.g. *Rhynchonellina*), cardinal processes (e.g. *Hemithyris*), fused hinge-plates (e.g. *Prionorhynchia*) or more complex crura (e.g. *Orbirhynchia*) may require new subfamilies. However, the classification of the rhynchonelloids is at the moment extremely incomplete and illogical, and much work needs to be done before it is desirable to erect further categories.

Rhynchonella s.s. may be regarded as a slightly specialized offshoot of the main stock of rhynchonelloids, its specialization taking the form of a paucicostate, cynocephalous shell, homoeomorphic with those belonging to *Pugnax*, *Homoeorhynchia*, and other genera.

POSSIBLY RELATED SPECIES

The following nominal species and subspecies have been associated with *R. loxia* by various authors and require individual consideration. Those marked with an asterisk are regarded by the author as probably belonging to *Rhynchonella* s.s., though it is by no means certain that they are all specifically distinct, and their internal characters have not been studied.

Homoeorhynchia acuta (J. Sowerby)

This species, which belongs to the Upper Pliensbachian (Middle Lias) of western Europe, has often been confused with *R. loxia*, as it was by Fischer himself (1843), Rouillier (1844), and Quenstedt (1885). The genus *Homoeorhynchia* has recently been revised (Ager 1956, p. 26) and its separation from *Rhynchonella* was there discussed. It is clear that, whatever may be the relationship between the two genera, the two species are quite distinct, though homoeomorphic in generalities. Similar homoeomorphs can be found among Palaeozoic rhynchonellids of the *Pugnax* group.

'*Rhynchonella*' *bidens* and '*R*'. *triplicata* (Phillips)

These names have been used by many authors for any sharply folded rhynchonellids with bi- or tri-costate folds respectively. They have recently been shown by the present author (op. cit., p. 40) to be synonyms of the west European Lower Jurassic form *Rhynchonelloidea lineata* (Young and Bird). Rouillier and Vossinsky (1847) used the above names for Upper Jurassic rhynchonellids near Moscow associated with *R. loxia.* They recognized that the bi-costate form was merely a variant of the tri-costate one and suggested, as an alternative to '*bidens*' the name *Terebratula triplicata subacuta* (op. cit., p. 376). There is, however, no more than a superficial resemblance to Phillips's Middle Liassic brachiopods from Yorkshire, and these Russian forms may be referred to the next species.

**Rhynchonella rouillieri* Eichwald

This name was proposed by Eichwald (1868) for the Russian Upper Jurassic forms which Rouillier and Vossinsky had referred to *T. bidens* Phillips. Later (1869, p. 1286) he came to the conclusion that the tri-costate forms called *T. triplicata* by Rouillier also belonged here.

Wisniewska (1932, p. 16) revised *R. rouillieri* and included it in *Rhynchonella* s.s. Gerasimov (1955, p. 218) also did this and showed it to be a close relation of *R. loxia*, with *R. rouillieri* var. *subacuta* Rouillier (see above) as the immediate predecessor of the type species. He also proposed a new name for the tri-costate variants—*R. rouillieri* var. *biplicata*.

Morphologically, *R. rouillieri* would seem to graduate into *R. loxia*, but Gerasimov has shown that it preceded the type species in time, being recorded from various levels in the Lower Volgian, whereas Fischer's species is strictly Upper Volgian. It differs from *R. loxia* in its larger size, more upright beak, and (most obviously) in the presence of two or three costae on its pronounced fold. The relationship between the two species may be compared with that between *Homoeorhynchia acuta* (see above) and *H. cynocephala* (Richard) (see Ager 1956), but whereas in *Rhynchonella* the forms with bi- and tri-costate folds preceded the unicostate type, in *Homoeorhynchia* the relationship was the other way round. Radial striae have been observed in examples of this species from Mnevniki and there can be no doubt at all that it belongs to *Rhynchonella* s.s. A typical example is shown on Pl. 1, figs. 4*a*, *c*.

**Rhynchonella malbosi* Pictet

Gerasimov observed (1955, p. 218) that *R. rouillieri* var. *biplicata* appeared to be very like *R. malbosi* var. *chomeracensis* Jacob and Fallot of the French Portlandian. He also compared the latter with *R. loxia*. In the absence of more evidence, it is impossible to be certain on the point, but this species may well be a contemporary western relation of the Russian forms and may also be related to *R. portlandica* Blake (see below).

**Rhynchonella lewinski* Wisniewska

This is another bi-costate, sharply folded form which can reasonably be regarded as belonging to *Rhynchonella* s.s., though Wisniewska (1932, p. 18) expressed doubts about this when she first described it, because of her lack of well-preserved specimens. She recorded it from the Volgian (Bononian) of Poland.

**Rhynchonella aptycha* (Fischer)

This form was named by Fischer in 1843 (p. 124). He referred to it as a small version of '*acuta*' (that being the name he was then using for *R. loxia*). It is obvious from his figures (op. cit., pl. 4, figs. 7–9) that it is merely a juvenile version of the type species, as was recognized by Rouillier (1844). D'Orbigny (*in* Murchison *et al.* 1845) used this name instead of *R. loxia*, apparently having overlooked Fischer's earlier paper.

**Rhynchonella canard* Fischer

In his 1809 paper Fischer distinguished *R. loxia* from two other species which had been figured by Bruguière (1797). Both of these Fischer included in *Rhynchonella*, but they appear to have been overlooked by later workers. The name *R. canard* was given to a rhynchonellid with a sharp, bi-costate fold. Bruguière has listed this as undetermined (op. cit., pl. 245, figs. 6*a–c*). This might possibly be conspecific with *R. rouillieri* but this is now impossible to prove.

**Rhynchonella aigle* Fischer

This is the second of the two forms named by Fischer from Bruguière's figures. It has a sharp, simple fold comparable to that of *R. loxia*. Fischer may have made a mistake here, for the figures he quotes (Bruguière, pl. 246, figs. 1*a*, *b*) are clearly identified by Bruguière (op. cit., p. 151) as *Terebratula spirifera* Lamarck. Fischer may have intended to refer to pl. 245, figs. 7*a*, *b* (i.e. the previous figures) which show a similar form, but which were noted by Bruguière as undetermined, like its predecessor discussed above. Again this form may be conspecific with some well-known species.

'*Terebratula*' *variabilis* Schlotheim

This is the most ubiquitous of all names in Mesozoic brachiopod studies. It was used by Fischer (1837, p. 147) to replace his own taxon *Rhynchonella loxia* and was subsequently used by other authors in this context. The original figures bear no resemblance whatever to *Rhynchonella* s.s. and the only specimens remaining in Schlotheim's collection with this name appear to belong to the genus *Gibbirhynchia* Buckman. The present author proposes to discuss this name further in the second part of his monograph of Liassic rhynchonellids.

'*Rhynchonella*' *subvariabilis* Davidson

This is the only species, apart from *R. loxia*, which Buckman (1918, p. 57) included in *Rhynchonella* s.s. This was founded chiefly, it would seem, on Davidson's remark (1852, p. 81) that its surface is '. . . minutely longitudinally striated'. Apart from this one character (which may not in fact be homologous), *R. subvariabilis* is a multicostate form quite unlike *R. loxia* in general appearance. Its inclusion in *Rhynchonella* is probably therefore quite unjustified.

**Rhynchonella portlandica* Blake

This is the only rhynchonellid known to the author in British strata comparable in age to the Volgian, and probably the only British rhynchonellid referrable to *Rhynchonella* s.s. It was described by Blake (1880, p. 234) from the Portland Sand of the Dorset coast, and his figured specimens are preserved in the British Museum (Natural History) (register numbers B. 52283–5). It is very much like *R. loxia* in general shape, being smooth with a strong, sharp dorsal fold and uniplication, and a flat-bottomed ventral sinus. Buckman (1918, p. 57) rejected it as a member of the genus *Rhynchonella* because of the absence of what he regarded as the all-important radial striae. This may be merely a matter of preservation. The syntypes differ from *R. loxia* in having a more convex ventral valve, a larger and more incurved beak, and usually three or four lateral costae on each side. Like other rhynchonellids of this form, *R. portlandica* includes variants having two or three costae in the fold. It is perhaps noteworthy that this species is associated on the Dorset coast with the ammonite *Zaraiskites*, which occurs also in the Lower Volgian of Mnevniki, near Khoroshevo.

Acknowledgements. The author is greatly indebted to Dr. P. A. Gerasimov of the Ministry of Geology of the U.S.S.R. for the gift of a number of specimens which made this study possible, and also for a copy of his recent monograph which has not otherwise reached this country. Professor A. N. Sokolskaya of the Academy of Sciences also kindly helped in this connexion. The author also wishes to thank Dr. H. M. Muir-Wood, Mr. R. V. Melville, and Mr. A. G. Brighton for the loan of specimens from the collections in their charge. Dr. Muir-Wood also discussed several points with the author and allowed him to examine sections of *R. loxia* made at the British Museum (Natural History). Finally the author would like to thank his wife for her critical reading of the manuscript and Mr. J. A. Gee for his usual invaluable photographic help.

This paper is a 'pre-Treatise' publication in connexion with the author's contribution on the Mesozoic and Cainozoic rhynchonelloids for the 'Treatise on Invertebrate Paleontology' at present being published in the U.S.A.

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UPPER VISÉAN GONIATITES FROM THE MANIFOLD VALLEY, NORTH STAFFORDSHIRE

by W. S. BISAT

ABSTRACT. *Goniatites warslowensis* sp. nov. and *Pronorites ludfordi* sp. nov. are described from the Bollandian (P_1c Zone) of North Staffordshire.

INTRODUCTION

A RICHLY fossiliferous limestone band has been found by Mr. A. Ludford and Dr. D. Parkinson in Warslow Brook in the Manifold valley. The fauna, which includes *Posidonia becheri* and brachiopods, is chiefly remarkable for the abundance of solid goniatites in a good state of preservation, and the finders have placed these in my hands for examination and description. The goniatites are here referred to a new species of *Goniatites* and one of *Pronorites*. The occurrence of several specimens of the latter genus is unusual. This new species of *Pronorites* has sutural characters intermediate between those of *P. cyclolobus* (Phillips) and *P.* (*Stenopronorites*) *uralensis* (Karpinsky).

The bed from which these specimens were collected occurs in the bank of Warslow Brook at the Warslow–Clayton footbridge. Although occasional goniatites have been previously collected from Warslow Brook by G. B. Alexander and by Hudson (1945, p. 322) the localities referred to in the last-mentioned paper appear to lie about 250 yards upstream from the footbridge, and at a lower horizon. This area is also included in the paper by Prentice on the Carboniferous Limestone of the Manifold valley (1951, p. 190).

It would appear from a comparison of the new species of *Goniatites* with specimens collected by Mr. E. W. J. Moore from Dinckley, Lancashire, and from Eire, that the horizon of this Warslow Brook fauna lies between those of *G. falcatus* and *G. elegans*. All the specimens described have been presented to the Geological Survey Museum, London, and all registration numbers quoted are those of specimens in that museum.

SYSTEMATIC DESCRIPTIONS

Goniatites warslowensis sp. nov.

Plate 3, figs. 1–3, 5–7; Plate 4, figs. 1–8

Holotype. Zl 5230, Pl. 4, fig. 7, text-fig. 1.

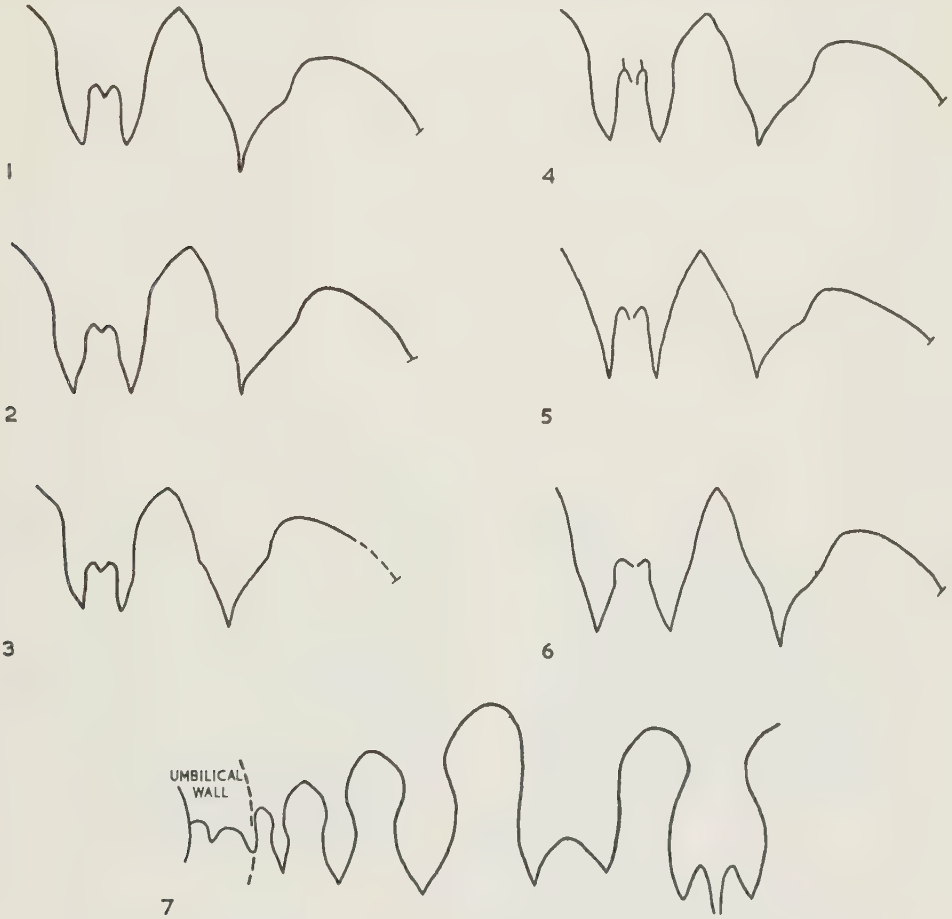
Paratypes. Zl 5225, Pl. 4, fig. 6, Zl 5226, Pl. 4, fig. 4, text-fig. 3; Zl 5227, Pl. 3, fig. 7, text-fig. 2; Zl 5248, Pl. 3, fig. 2; Zl 5311, Pl. 3, fig. 5.

Locality. Warslow Brook at Warslow to Clayton footbridge, Manifold valley, North Staffordshire.

[Palaeontology, Vol. 1, Part 1, 1957, pp. 16–21, pls. 3–4]

Horizon. Upper Viséan, Bollandian, P_1c Zone, probably between the horizons of *G. falcatus* and *G. elegans.*

Description. The species varies considerably in the characters of the suture line, and also in shape, and may be divided on these variations into four groups which tend to grade one into the other:



TEXT-FIGS. 1–7

Figs. 1–6. *Goniatites warslowensis* sp. nov. 1, Zl 5230, holotype, suture at 15 mm. diam. ×4·1. 2, Zl 5227, paratype, suture at 17 mm. diam. ×3·75. 3, Zl 5226, paratype, suture at 14½ mm. diam. ×4·37. 4, Zl 5224, suture at 18 mm. diam. ×3·44. 5, Zl 5239, suture at 30 mm. diam. ×2·08. 6, Zl 5231, suture at 22 mm. diam. ×2·81.

Fig. 7. *Pronorites ludfordi* sp. nov. Zl 5234, paratype, suture at 25 mm. diam. ×6·25, 6th lateral lobe drawn from holotype, Zl 5233.

(*a*) A globose form with wide depressed venter having a thickness equal to the diameter at 15 mm., and with open umbilicus with rounded margin. The sutures, which are rather crowded (about 18–20 to the whorl), have ventral lobes with cheeks markedly inturned towards the base. This ventral lobe varies considerably in width in different specimens, but there is a tendency for the cheeks to be upright in the young and to diverge more noticeably in later life (see Zl 5230). To this form, which is the most distinctive of the four groups, belong the holotype and above-cited paratypes.

(*b*) A subglobose form in which the inturned portion at the base of the cheeks of the ventral lobe is shorter and the ventral lobe has a more upright appearance. To this group belong Zl 5224, Pl. 3, fig. 1, text-fig. 4; Zl 5229, Pl. 4, fig. 2; Zl 5241, Pl. 4, fig. 3; Zl 5650, Pl. 4, fig. 1; and Zl 5651.

(*c*) A compressed form with comparatively narrow base to the ventral lobe, which has cheeks which are nearly straight or slightly sinuous or slightly convex on the inner surface, such as Zl 5228, Pl. 4, fig. 5, Zl 5239, Pl. 4, fig. 8, text-fig. 5, Zl 5240, Pl. 3, fig. 6.

(*d*) A compressed form in which the cheeks of the ventral lobe become widely divergent with straight-sided cheeks in the adult, and the ventral lobe has a wide base, such as Zl 5231, Pl. 3, fig. 3, and Zl 5652–3.

The lateral lobe of the suture line is of medium width, with sinuous cheeks (except in Zl 5240) and with a very narrow basal spike, which increases in prominence during ontogeny, becoming a marked channel-like feature in later life. (See Zl 5231, Pl. 3, fig. 3; Zl 5650, Pl. 4, fig. 1.)

The ornament consists of both transverse and spiral striae. The transverse striae are crenulate in the young, but the crenulations become feebler with age. The transverse and spiral striae are of approximately equal strength. In the young at about 9 mm. diameter (Zl 5248, Pl. 3, fig. 2) the transverse striae emerge from the umbilicus approximately radially, bend somewhat backward on the lower half of the flank, and then sweep boldly and broadly forward over the latero-ventral shoulder, flattening to normal over the venter. This direction of the striae is reminiscent of that of *G. waddingtoni* Bisat (86971), and of other variants of the *G. sphaericostriatus* stock collected by Mr. E. W. J. Moore in Co. Leitrim, Eire. With increasing age the above bold forward sweep rapidly diminishes, and the transverse striae emerge radially from the umbilicus, bend somewhat backward on the upper half of the flank (Zl 5311, Pl. 3, fig. 5) and flatten to normal over the venter (Zl 5227, Pl. 3, fig. 7).

Most of the specimens on which the above description is based are rather small, being of the order of 15–25 mm. diameter, but fragmentary specimens of larger diameter occur, one of which (Zl 5649) with a diameter of about 42 mm., although badly preserved, shows a broad lingua and hyponomic sinus, and somewhat undulating transverse ornament on the flank, which develops wrinkles on the lingua. The hyponomic sinus evidently develops late in life as there is no sign of it up to 25 mm. diameter.

Constrictions on the internal cast are very rare. The umbilicus is always open. It has a rounded or sub-acute border, and is generally about 25 per cent. of the diameter,

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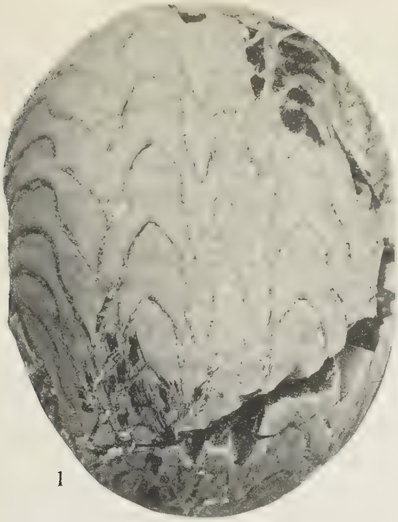
EXPLANATION OF PLATE 3

All the specimens are from the Upper Viséan, P_1c Zone, Warslow Brook, North Staffordshire.

Figs. 1–3, 5–7. *Goniatites warslowensis* sp. nov. 1, Zl 5224, ×3·7. 2, Zl 5248, ×5·7, paratype showing flank ornament in the young. 3, Zl 5321, ×3·7. 5, Zl 5311, ×5·7. 6, Zl 5240, ×3·7. 7, Zl 5227, ×5·7, paratype showing ventral ornament at 25 mm. diameter.

Fig. 4. *Pronorites ludfordi* sp. nov., holotype, Zl 5233, ×3·7.



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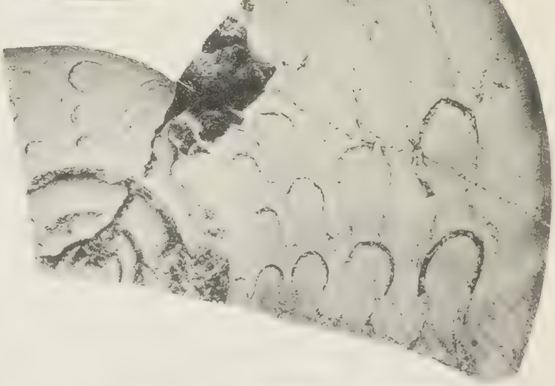

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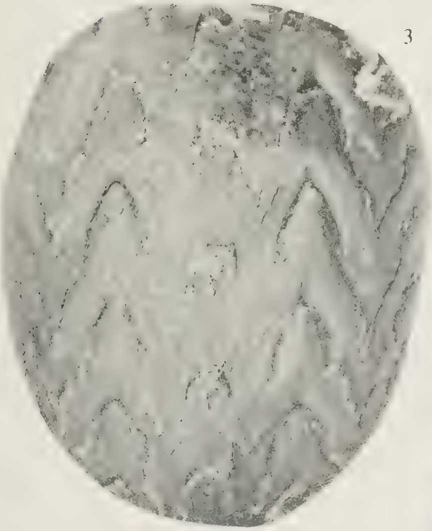

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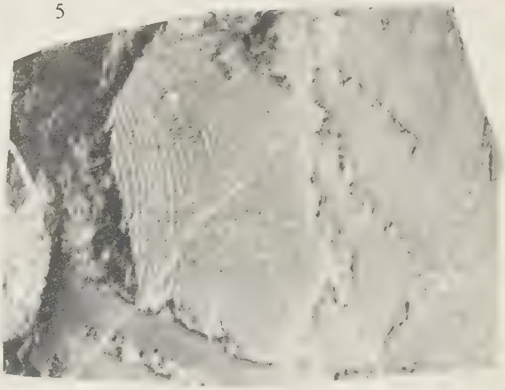

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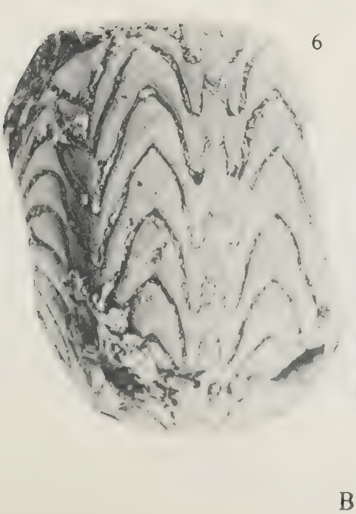

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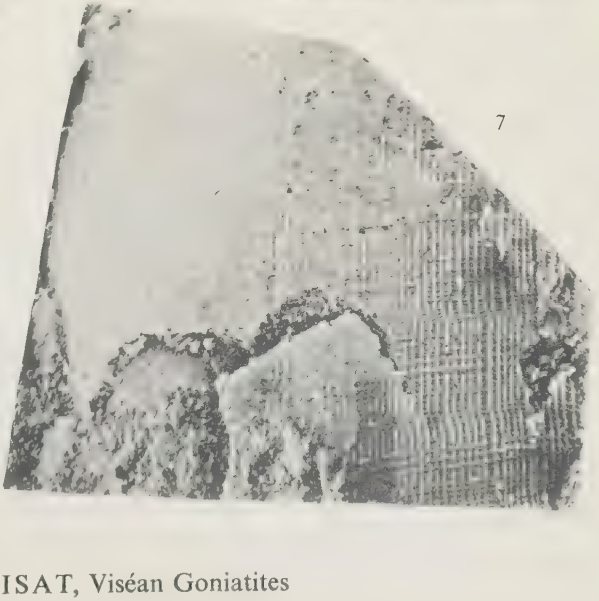

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BISAT, Viséan Goniatites

though it is somewhat greater in young specimens, and tends to be rather smaller in the more compressed forms.

Remarks. It would appear from the character of the suture lines, and from the stratigraphy so far as that can be deduced, that the horizon of this species lies in the Bollandian above that of *G. falcatus* and below that of *G. elegans*. The Warslow Brook specimen Zl 5230 compares well in shape and suture line with Zl 4073 collected by Mr. E. W. J. Moore from near Loughaphonta, Co. Leitrim, Eire, at a horizon above *G. falcatus* and below a series of beds containing *G. sphaericostriatus* and allied forms. The Warslow Brook specimen also comes close to G.S. 86397 collected by Mr. Moore at Dinckley, R. Ribble, Lancashire, from an horizon between *G. falcatus* and *G. elegans*.

Apart from the above specimens the nearest species to *G. warslowensis* so far as similarity of suture lines is a guide appears to be the form of *G. falcatus* which occurs at horizon Co 6 (of Bisat 1952) Cowdale Clough (59612) and the similarly sutured specimen from M3 Little Mearley Clough, Pendle Hill (85656) figured by the writer (1952, p. 172, fig. 3*e*). There is also close similarity between the form of *G. warslowensis* with divergent cheeks to the ventral lobe (Zl 5231, Pl. 3, fig. 3) and the suture line of a specimen of *G. falcatus* from Dinckley (85657) figured op. cit., fig. 3*a*. Similarities also exist between the suture lines of *G. warslowensis* and those of *G. sphaericostriatus* from Co. Leitrim. Compare, for instance, that of Zl 5230 with Zl 5646 and 5648 from Co. Leitrim, the basal spike to the lateral lobe in the Irish specimens being less of a noticeable feature than in *G. warslowensis*, but otherwise there is the same general type of suture line, and similar variations in the character of the ventral lobe in different specimens. In *G. sphaericostriatus*, however, the spiral striae become dominant, unlike *G. warslowensis*.

G. intermedius Kobold 1933 *non* Brown 1841 which apparently comes from a lower horizon than *G. warslowensis*, has a very similar type of ornament (Kobold 1933, pl. 22, fig. 3), and the lateral lobes of the suture lines of the two species are not dissimilar (Kobold 1933, pl. 22, fig. 2) but the two species differ in the size of the umbilicus, which in *intermedius* is only $\frac{1}{9}$th of the diameter (Kobold 1933, p. 487), and the ventral lobe of *intermedius* does not seem to have been clearly seen.

Pronorites ludfordi sp. nov.

Plate 3, fig. 4

Holotype. Zl 5233, Pl. 3, fig. 4. *Paratypes.* Zl 5232; Zl 5234, text-fig. 7.
Locality and horizon. As for *G. warslowensis*.

Description. This species differs from *P. cyclolobus* (Phillips) as figured by Foord and Crick (1897, p. 261, fig. 125) in that the 4th lateral lobe at a whorl height of 9 mm. (diameter *c.* 25 mm.) is deeper and narrower and lies wholly on the flank, the 5th lateral lobe is on the umbilical crest, whilst there is a 6th lateral lobe on the umbilical wall seen in Zl 5233 at a whorl height of 12 mm. The suture line shows an approach to that of *Pronorites* (*Stenopronorites*) *uralensis* (Karpinsky), but this latter form has the 5th lateral lobe on the edge of the flank at 9½ mm. whorl height, and also the ventral lobe lacks the constriction or neck near its mouth which is characteristic of both *cyclolobus* and *ludfordi*. *P. uralensis* is stated to be of Namurian age.

Traces of obtuse backwardly directed plications may be seen on the flank of the internal cast of *P. ludfordi*, and this type of ornament appears to be characteristic of the family. Similar ornament may be seen on two specimens of *Pronorites* (Zl 5977–8) collected by Mr. Moore at Cowdale Clough, horizon Co 5 of Bisat 1952, and there is a good illustration of it in a much later species, *Uddenites oweni* figured by Miller and Downs (1950, pl. 31, fig. 4).

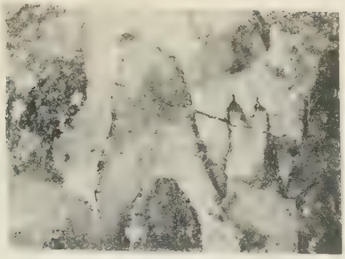
Remarks. The specimen of *Pronorites* from Chebket el Hamra, E. Morocco, mentioned and figured by Delépine (1941, p. 48, pl. 5, figs. 3, 4, text-fig. 8, p. 51), and referred by him to *Stenopronorites uralensis*, differs from that species in having a ventral lobe constricted to a neck near its mouth. Whilst it agrees with *P. cyclolobus* and *P. ludfordi* in this feature, it has a smaller umbilicus than either of these two species and appear to come closest to a specimen (Zl 5749) collected by Mr. Moore from beneath the *G. striatus* beds near Loughaphonta, Eire. This last specimen at a diameter of 33 mm. has the 5th lateral lobe high up on the umbilical wall, and there are traces of a 6th lateral lobe lower down the umbilical wall. One may note here that the *Pronorites* from Chebket el Hamra was collected by Owodenko (1946, p. 47) not *in situ* from an area which otherwise had only yielded such Upper Viséan species as *Posidonia becheri*, *G. falcatus*, *Beyrichoceratoides*, and lower forms. Two other species of *Pronorites* should here be mentioned. *P. reyi*, Dollé (1912, p. 256, pl. 7, fig. 3, text-fig. iii–3) has a much wider umbilicus than *P. ludfordi*, and in *P. reyi* the 5th lateral lobe is apparently hardly developed, and there is no evidence for a 6th lateral lobe. *P. barroisi* Karpinsky (= *Goniatites cyclolobus* Phillips of Barrois 1882, pl. 14, fig. 2) comes near to the Moroccan and Irish specimens referred to above in shape and umbilicus but has a narrow straight-sided ventral lobe. It presumably occurs in the Upper Viséan of Spain, but this type of ventral lobe is otherwise unknown in *Pronorites* of Viséan age.

Acknowledgements. The writer is much indebted to Dr. W. H. C. Ramsbottom and Dr. F. Hodson for the photographs which illustrate this paper, and to Miss E. W. Andrews for assistance given in the preparation of the suture line drawings for reproduction.

EXPLANATION OF PLATE 4

All the specimens are from the Upper Viséan, $\mathrm{P_{1}c}$ Zone, Warslow Brook, North Staffordshire.

Figs. 1–8. *Goniatites warslowensis* sp. nov., all figures ×3·7. 1, Zl 5650. 2, Zl 5229. 3, Zl 5241. 4, Zl 5226, paratype. 5, Zl 5228. 6, Zl 5225, paratype. 7, Zl 5230, holotype. 8, Zl 5239.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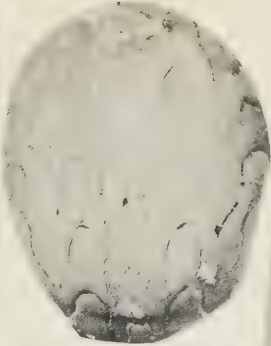
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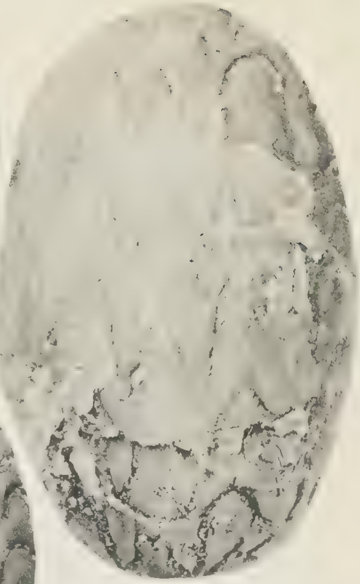
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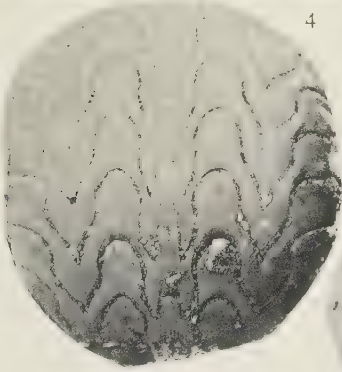
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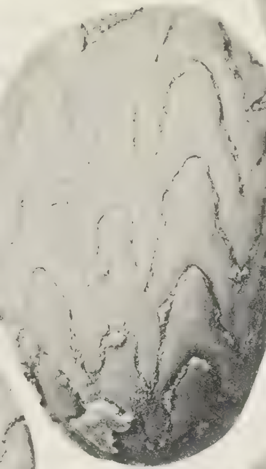
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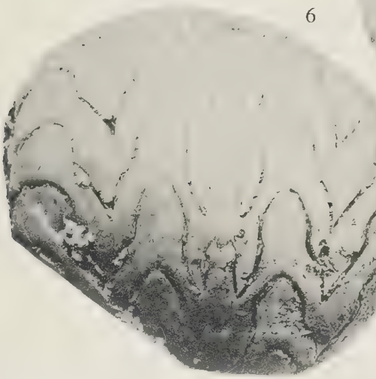
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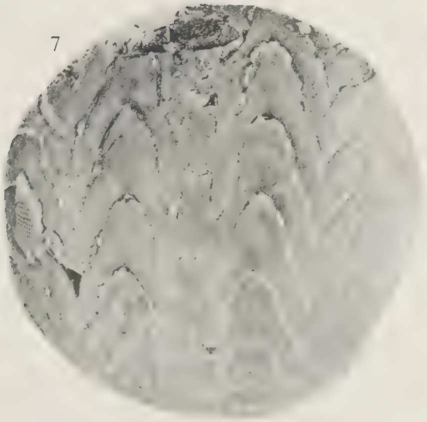
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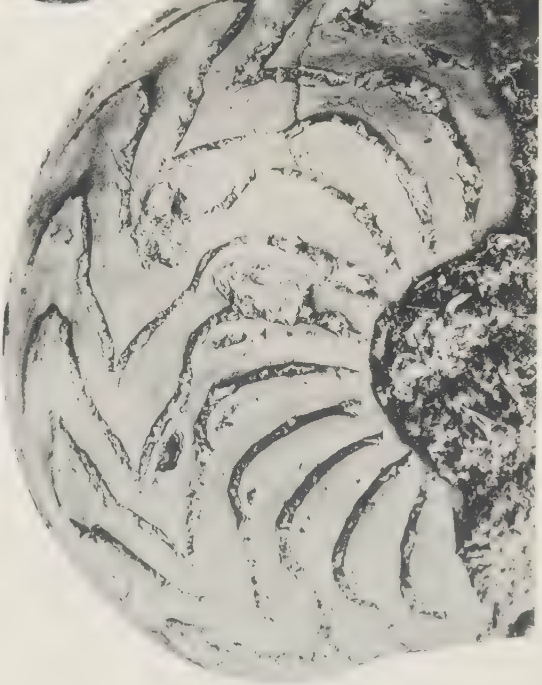
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THE TYPE-SPECIES OF THE GENUS *GIRVANELLA* (CALCAREOUS ALGAE)

by ALAN WOOD

ABSTRACT. Topotype Ordovician material containing *Girvanella problematica* Nicholson and Etheridge has been studied, several species being found to occur together. The genus is redefined and the limits of variation of the type species indicated.

INTRODUCTION

THE genus *Girvanella* was founded by Nicholson and Etheridge (1878) to include aggregations of tiny tubes with granular walls occurring in the 'Craighead Limestone' (later called the Stinchar Limestone) of Tramitchell, near Girvan, south Scotland. These beds are of Upper Ordovician age. One small illustration was given, reproduced as Pl. 5, fig. 1, of the present paper. The original generic diagnosis runs: 'Microscopic tubuli, with arenaceous or calcareous (?) walls, flexuous or contorted, circular in section, forming loosely compacted masses. The tubes apparently simple cylinders, without perforations in their sides, and destitute of internal partitions or other structures of a similar kind.' One species, *G. problematica*, was established 'for convenience' sake'. The authors, after seeking the advice of H. B. Brady, ascribed the genus to the Foraminifera.

It was soon found that similar forms occurred at other horizons. Wethered (1889, 1890) described new species from the Silurian, Carboniferous, and Jurassic. Seely (1885) and Bornemann (1886) erected the genera *Stephochetus* and *Siphonema*, considered to be a calcareous sponge and a calcareous alga respectively, which were shown by Hinde (1887) to be synonyms of *Girvanella*. The genus is now known to be world-wide in distribution and has been recorded from rocks of all ages from Cambrian to Cretaceous (Pia 1927).

Concerning the systematic position of this fossil, Brady (1884) stated that the generic and specific characters cited for *Girvanella problematica* agreed so well with those of the recent foraminifer *Hyperammina vagans* Brady, except for the diameter of the tubes, that 'it seems scarcely worth while to recognize these trifling differences as a basis of generic distinction'. Rhumbler (1895) likewise regarded this genus as a foraminifer; he was inclined to consider *Girvanella* as the basic type, from which *Ammodiscus* was derived, and he erected a new subfamily Girvanellinae to include *Girvanella*, *Tolypammina*, and *Syringammina*.

Already Bornemann (1886) had described his new genus *Siphonema* as a calcareous alga, and in 1891 Rothpletz considered *Girvanella* to belong to this group, a view followed by Brown (1894) and Seward (1898). There can be little doubt that this position is correct (subject to the reservation made on p. 27). The genus occurs in nodules similar to those of other calcareous algae, and in the same facies. Furthermore, the walls of the tubes are composed of typical 'algal dust'. When compared with the tubes constructed by agglutinating foraminifera, there is a contrast in mode of growth. The foraminiferal tubes are irregularly constricted at intervals, probably at periods when the food supply

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was restricted, while the tubes of *Girvanella* maintain a more even diameter, quite possibly due to uniform assimilation over the whole surface.

As such the genus has considerable value as a facies indicator, the nodules and pisoliths formed by its growth indicating shallow clear water. By comparison with modern algal balls these forms cannot have flourished below depths of about 30 fathoms. Often, as in the case of the well-known *Girvanella* Band in the Lower Carboniferous of northern England, these fossils show the sea to have been shallow and of uniform depth over an area of hundreds of square miles.

THE TYPE OF *GIRVANELLA*

The original description of *G. problematica*, the type species by monotypy, runs: 'Tubes from $\frac{1}{600}$th to $\frac{1}{700}$th of an inch in diameter, not observed to taper, twisted together in loosely reticulate or vermiculate aggregations of a rounded or irregular shape, which seem to be mostly from $\frac{1}{20}$th to $\frac{1}{10}$th of an inch across'. In the discussion which followed this diagnosis, which was mainly concerned with the zoological affinities of the fossil, the important statement was made that the tubes were always so loosely reticulated that the interstices of the mass were filled up with transparent calcite 'readily distinguishable from the more opaque and granular matrix which surrounds them'. The genus was later redescribed by Nicholson (1888) and by Wethered (1890) in much more accessible publications, and in 1891 Rothpletz, who had received specimens from Nicholson himself, stated that the tubes of the typical *Girvanella* showed dichotomous branching, and that there were two sets of tubes visible, distinguished by their different size. One group measured 6–9, the other 9–15μ in diameter, and he considered that there was a direct connexion ('unmittelbarer Zusammenhang') between the two. Already there was a considerable discrepancy between the quoted diameters for the tubes of this species; Nicholson and Etheridge's figures correspond to 35–42μ, Nicholson in 1888 gave a range between $\frac{1}{25}$ and $\frac{1}{60}$ mm. with a most common size of $\frac{1}{45}$ mm. (17–40μ, commonly 22μ), and Rothpletz's figures were smaller again.

Later authors passed over this discrepancy. Høeg (1932), for instance, describing forms of *G. problematica* from the Trondheim area, laid emphasis on the aggregation and mode of preservation of the filaments. He distinguished three groups, *typicalis*, occurring in crowded masses of threads, often with diffuse outlines, with a diameter of 16–20μ, *lumbricalis* occurring sparsely scattered or loosely aggregated, with a diameter of 14–17μ, exceptionally 20μ, and *moniliformis* which occurred dispersedly in a calcareous matrix, and often showed a prevailing direction of tubes in the colony, with a diameter of 20–26μ, sometimes larger. A further discussion of *G. problematica* was given by Lewis (1942) who concluded that all the forms, ranging in diameter from 11 to 26μ (rarely 30μ), were varieties of one species, within which American Ordovician *Girvanella* spp., for instance *G. ocellata* (Seely), could be accommodated.

Part of the discrepancy between the various descriptions may be due to the fact that most specimens from Girvan studied by later authors, including those figured by Nicholson in 1888, did not come from Tramitchell, but from the much more accessible Craighead Quarry near the town. To clear up the confusion search has been made for the original slides of 1878. Unfortunately Nicholson's collection was destroyed by fire in Aberdeen, and the only slide in the British Museum (N.H.) collections from Tramitchell (reg. no. V. 20734), though presented by Nicholson, does not contain the type specimen. Nineteen different aggregations of algae are seen in the slide, and they can be divided into three or four species on size of tube and mode of aggregation. The slide is thick and the boundaries between the species are uncertain and difficult to draw. Accordingly a fresh collection has been made from Tramitchell (now Tormitchell) Quarry and through the whole section exposed of the Stinchar Limestone at the typical locality, Benan Burn, south of Girvan. Over 100 thin sections were made containing very many algae. Camera lucida drawings were found to be unsuitable and finally 375 quarter-plate photographs of different aggregates at a uniform magnification of 200 diameters were taken as negatives on bromide paper, and these made a comparative study possible.

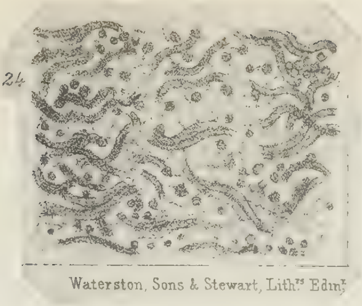
RESULTS OF STUDY OF NEW SPECIMENS FROM GIRVAN

Mode of aggregation of the tubes. Very considerable variation exists. Many specimens show tubuli freely twisting about within areas of clear crystalline calcite. Others are preserved in dark algal dust, and their boundaries are difficult to discern. Among the largest tubuli are many whose mode of aggregation recalls that of the type figure (Pl. 5, fig. 1), vermiform tubes, gently curving and rarely in contact. Other tubuli are more strongly curved and closely aggregated. Occasionally tubes run subparallel, being in every other feature identical with the more flexuous type. On the whole, however, those specimens having the widest tube diameter are less twisted and contorted than the slimmer tubes, though a few specimens of the large species were found showing the closely adpressed and twisted tubes hitherto considered typical of *Girvanella* (Pl. 5, fig. 4). Branching has been seen several times and in the large species is never of symmetrical dichotomous type (Pl. 6 , figs. 1, 2). No passage between tubes of one diameter and one of another has been seen, and the tubes of one aggregation are generally of uniform diameter, though there are exceptions.

Diameter of the tubes. Careful measurement of the diameter of the tubes showed that tubes of all sizes intermediate between the largest and smallest occurred. Though it was possible to recognize 'species' by observation alone, their boundaries were extraordinarily difficult to draw. Measurement of several hundred tubes from different aggregations was of no avail; eventually it was realized that measurements of longitudinal sections of tubes whose diameter was less than the thickness of the slide must lead to inaccurate results. Furthermore, if these algae are actually preserved as moulds in a fine granular calcareous matrix precipitated by their own life-processes, the 'wall' may well vary in thickness according to local conditions. Accordingly measurement was restricted to cross-sections, and all the well-preserved cross-sections in the photographs

EXPLANATION OF PLATE 5

Figs. 1–5. *Girvanella problematica* Nicholson and Etheridge. 1, Reproduction of Nicholson and Etheridge's original figure, 'Portion of a slice of limestone showing the tubes of *G. problematica.* Tramitchell. ×50 (Coll. H. A. Nicholson).' 2, Neotype, B.M. (N.H.) reg. no. V. 34566, ×120, Stinchar Limestone, Tormitchell Quarry, Girvan. 3, Small aggregation showing cross-sections and possible cell walls, ×87. Stinchar Limestone, Benan Burn, Girvan. 4, Aggregation closely packed with meandering tubes, ×87½. Stinchar Limestone, Benan Burn, Girvan. 5, Subparallel tubes with possible repeated branching at top, ×87½. Stinchar Limestone, Benan Burn, Girvan.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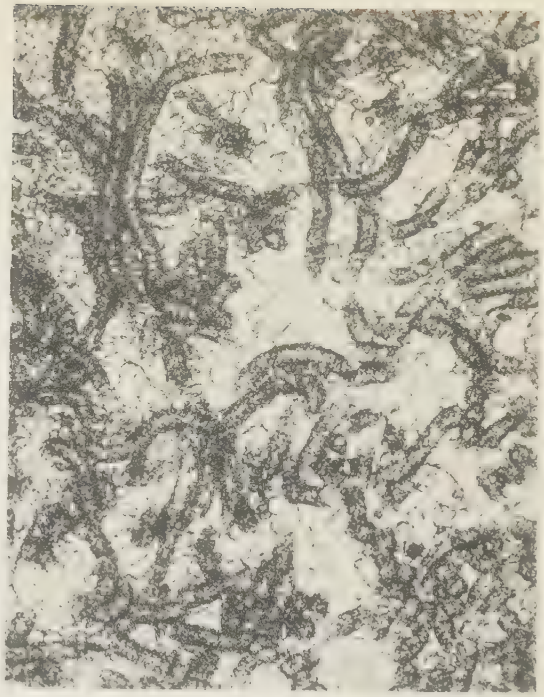

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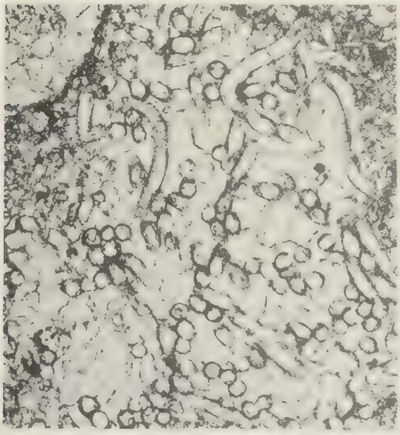

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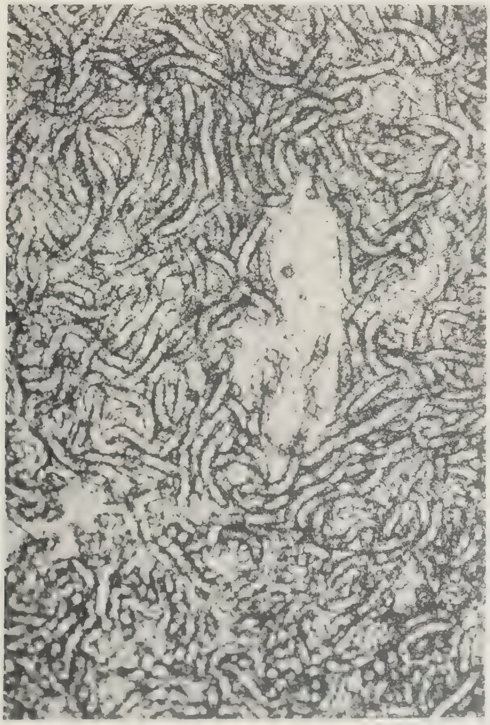

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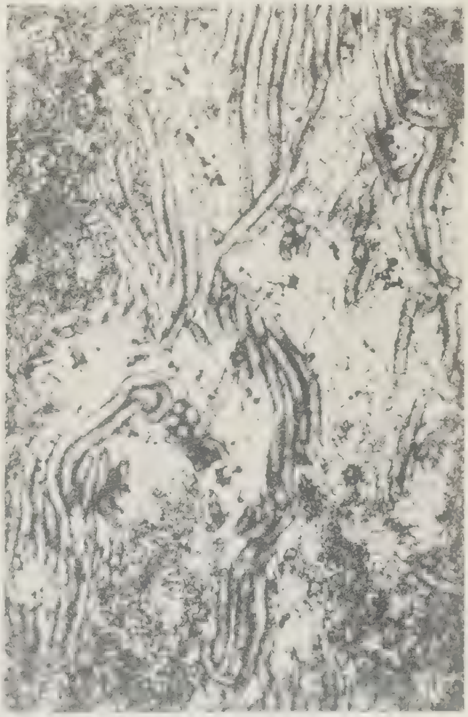

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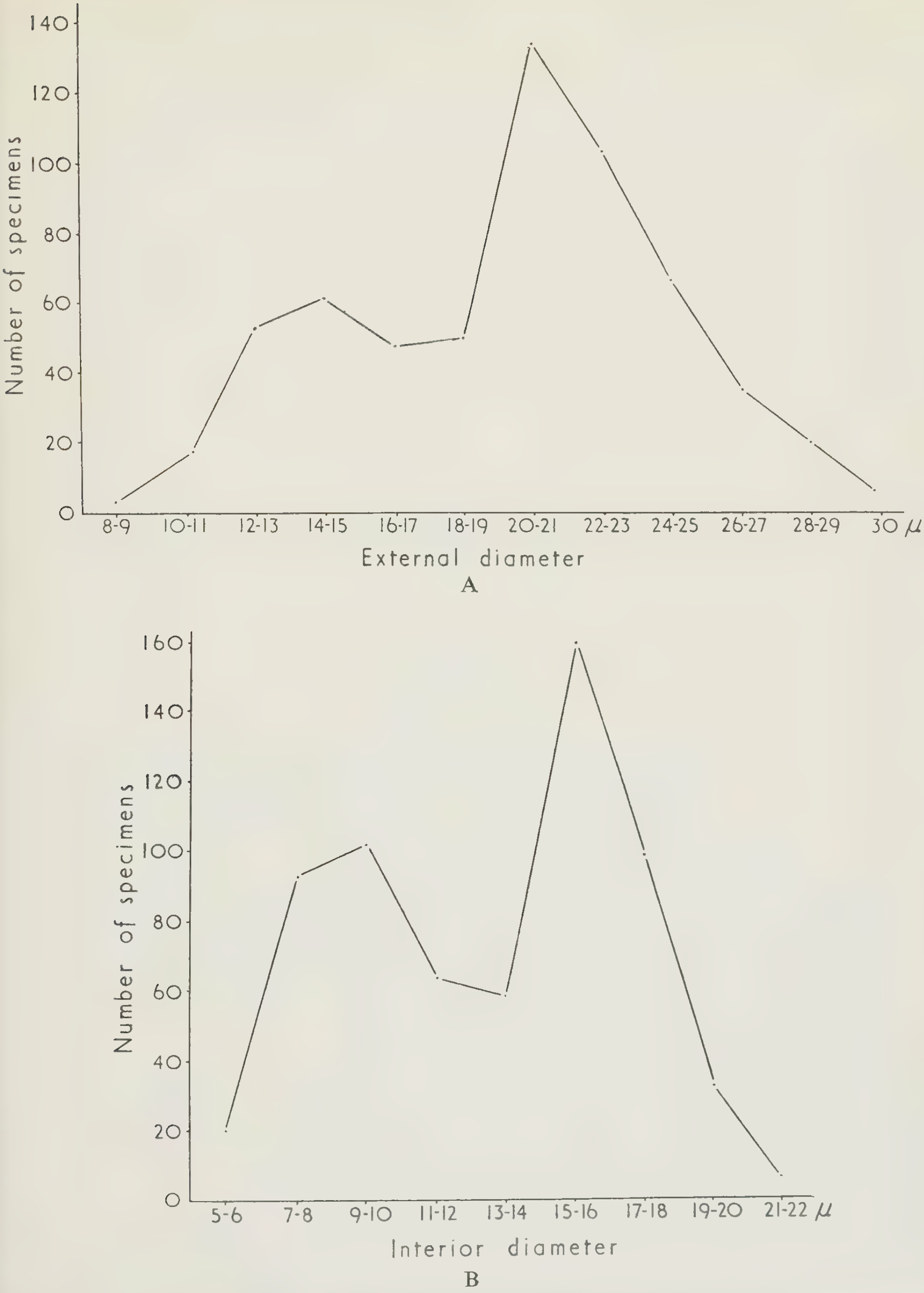
WOOD, *Girvanella*



TEXT-FIG. 1. A. Graph of external diameter of circular cross-sections of tubuli of *Girvanella*. Stinchar Limestone, Tramitchell and Benan Burn. B. Graph of internal diameter of circular cross-sections of *Girvanella* tubuli. Stinchar Limestone, Tramitchell and Benan Burn.

were measured, their diameter being estimated to $\frac{1}{5}$th of a millimetre, representing 1μ. Often a single tube did not show both exterior and interior clearly, so that the number of readings in the two graphs (text-fig. 1) is different. Inspection of these graphs shows that tubes of every internal diameter from 5 to 22μ, and every external diameter from 8 to 30μ, occur in these slides. Maxima occur at an external diameter of $20–21\mu$ (internal diameter $15–16\mu$) and $14–15\mu$ (internal diameter $9–10\mu$). By inspection it can be seen that the graph of internal diameters is more compact than that of external diameters, and that its maxima are more clearly marked, and more symmetrical. The graph of external diameters is skewed towards the right, as can be seen especially in the range from 20 to 30μ. This is presumably due to variation in the amount of precipitation of calcium carbonate on the exterior of the thread. The operation of the same factor has caused the gap between the smaller and larger group to be partially filled. It is clear that readings of the internal diameter of the tubes are more reliable.

Even when the internal diameters are measured, however, there is a considerable number of specimens intermediate in diameter between the two peaks on the graph. To account for the continuity of the graph, we must assume that either the two species are highly variable, in response perhaps to outward conditions, or there are five or six, or even more, species present which are being confounded. Though the evidence is not good enough to decide between these possibilities it is clear that at least two species occur, with the average diameters previously cited. The larger of these corresponds to Nicholson and Etheridge's original description, and is redefined below.

SYSTEMATIC DESCRIPTION

Girvanella problematica Nicholson and Etheridge 1878

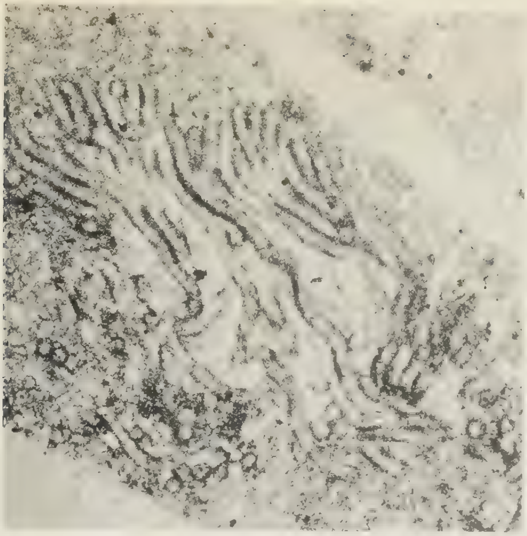
Plates 5 and 6

Diagnosis. Tubes flexuous, not observed to taper, rarely branching, twisted together in loosely aggregated masses, less commonly closely packed. Average external diameter of tubes $21–22\mu$, ranging from 18 to 25 (rarely 30)μ, average internal diameter of tubes $15–16\mu$, ranging from 13 to 20 (rarely 22)μ.

Observations. Branching has been observed on several occasions. A single branch at a wide angle is shown in Pl. 6, fig. 2, while repeated branching occurs in the specimen figured on Pl. 6, fig. 1. Here the whole *Girvanella* is lying more or less parallel to a shell fragment (seen in the lower left-hand corner) and is branching away from it. The repeated branching strongly suggests growth out into a favourable environment. All the branches end at the same level. Cross walls appear to occur in some well-preserved specimens, a feature already observed by Frémy and Dangeard (1935) in *G. symplocoidea* of the Jurassic. In the specimen figured in Pl. 5, fig. 3 the possible cell walls are clearly seen in the upper part of the photograph. The circular cross-section of the tubes, the thickness of their walls, and their uniformity in size can also be appreciated.

EXPLANATION OF PLATE 6

Figs. 1–4. *Girvanella problematica* Nicholson and Etheridge. 1, Repeated branching, ×87½. Stinchar Limestone, Benan Burn, Girvan. 2, Single branch in a lax aggregation, ×200. Top bed of Stinchar Limestone, Benan Burn, Girvan. 3, *G. problematica* inside a *Saccamminopsis* test, ×87½. Stinchar Limestone, Benan Burn, Girvan.



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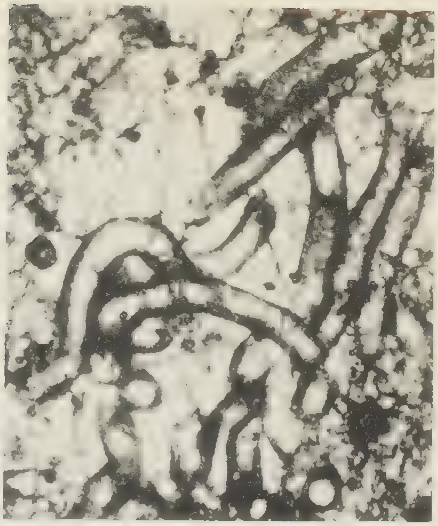

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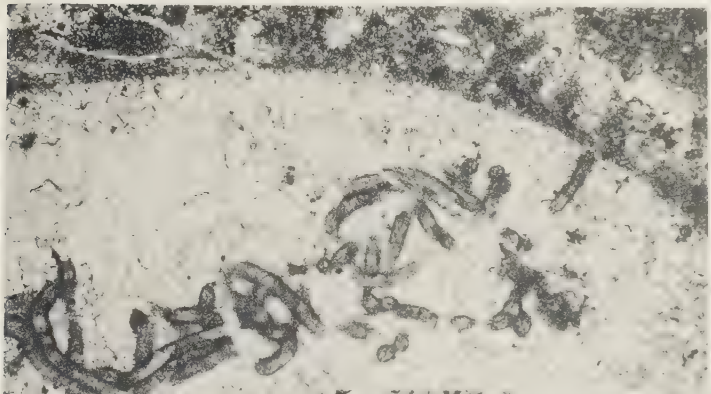

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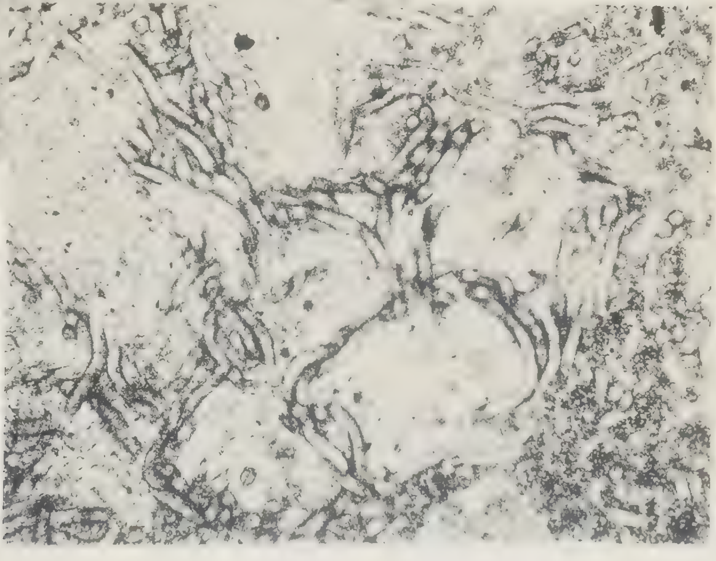

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WOOD, *Girvanella*

The specimen figured on Pl. 6, fig. 3 is unusual in that the *Girvanella* threads occur inside the middle chamber of a three-chambered *Saccamminopsis* test. The tubular connexions with the chambers in front and behind are complete, and the initial chamber is filled with clear crystalline calcite. The lower part of the chamber in which the *Girvanella* occurs is filled with finer grained rather murky calcite partially shown in the figure, the *Girvanella* threads occurring in the upper, more crystalline portion. The last chamber is broken, its contents merging with the matrix. If *Girvanella* was a green or blue-green alga it would seem to be impossible for it to flourish in the dark, inside the chamber of a foraminifer. The tubular connexion between the two last chambers is just large enough to allow the *Girvanella* to slip through, so that it may be a detrital fragment. However, one piece of evidence points the other way. A single thread of *Girvanella*, seen on the right of the photograph, appears to traverse the wall of the foraminiferal test. This is the only fact observed that supports the view of Cayeux (1909) that *Girvanella* was a boring organism, all other observations being in accord with a free mode of life. However, if other specimens are found in a similar situation the systematic position of *Girvanella* will have to be reviewed.

The loose packing of the threads is a point of difference from *Girvanella* spp. described from other horizons, as is the fact that the threads quite commonly grow subparallel (Pl. 5, fig. 5). Occasional closely packed specimens with contorted tubes do occur (Pl. 5, fig. 4). These may be cut parallel to the surface on which the algae were growing. The sharp boundaries of many aggregations may be interpreted as detrital rounding, which suggests that they were soon lithified.

It is unfortunate that Høeg (1932) gave the name *typicalis* to one of his forms of *G. problematica*, since this does not correspond exactly to the original description and figure. The form he termed *moniliformis* is, however, very close to and probably identical with the true *G. problematica*. However, the alga is so protean that many other forms might be distinguished, probably related to micro-environments.

Neotype (here chosen). The specimen shown on Pl. 5, fig. 2, now in the British Museum (N.H.) collection, reg. number V. 34566.

Horizon and locality. Stinchar Limestone (Ordovician, Llandeilo), Tormitchell, Girvan, Ayrshire.

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THE CRETACEOUS AMMONITE GENUS *LEYMERIELLA*, WITH A SYSTEMATIC ACCOUNT OF ITS BRITISH OCCURRENCES

by RAYMOND CASEY

ABSTRACT. Ammonites of the genus *Leymeriella* Jacob characterize the Northern Hemisphere and are found in neritic deposits of Lower Albian age extending from the Urals to east Greenland. Known occurrences are restricted to the Zone of *Leymeriella tardefurcata*. Investigation of anomalous records of *Leymeriella* in the overlying Zone of *Douvilleiceras mammillatum* discloses that the classic 'Mammillatum' bed of the Ardennes and Meuse Departments of France, which furnished d'Orbigny with much type material, is a condensed deposit in which elements of both Tardefurcata and Mammillatum age are combined. Account is taken of 18 species and 3 varieties of *Leymeriella* (including the subgenus *Epileymeriella* Breistroffer), of which 4 species and 1 variety are new, and 4 species of *Proleymeriella* Breistroffer, 1 new. Systematic treatment is given 7 species and 3 varieties of *Leymeriella* of British provenance.

Mode of coiling, ontogenetic development of the septal sutures, and certain sculptural features indicate that the affinities of *Leymeriella* lie with the Lyelliceratidae (Acanthocerataceae) rather than with the Hoplitidae (Hoplitaceae) to which it has been generally attached. It is believed that *Leymeriella* provides the key to the origin of the great ammonite superfamily Acanthocerataceae. An eruptive phase of evolution at the beginning of the Albian is postulated in which the Lyelliceratidae (including Leymeriellinae), Brancoceratidae, and Mojsisovicsiidae are conceived as simultaneous and rapidly differentiating offshoots of the Desmoceratid *Callizoniceras*. Support for this hypothesis is given by '*Hoplites*' *haidaquensis* Whiteaves, from the Albian of the Queen Charlotte Islands, a member of the Lyelliceratid-Brancoceratid complex for which the nominal genus *Pseudoleymeriella* is proposed. It is suggested that the Acanthocerataceae and the Hoplitaceae may represent synchronous radiations from the Lytocerataceae and Phyllocerataceae respectively.

Leymeriellinae and Hoplitinae may have been mutually exclusive, the one shunning areas favourable to the other. The apparent extinction of *Leymeriella* coincided with the appearance in Europe of new, virile Hoplitid stocks in the Mammillatum Zone.

INTRODUCTION

Leymeriella is a closely integrated group of Lower Cretaceous ammonites whose evolution, geographic dispersal, and extinction have features of unusual interest to the palaeontologist. Confined to the base of the Albian, yet with a wide distribution throughout Europe, it forms an excellent horizon-maker and its two principal species, *L. tardefurcata* (d'Orb.) and *L. regularis* (Brug.), have figured prominently in literature relating to Albian stratigraphy and zonal classification. Since the time of its description by Jacob (1907, 1908) the genus has been studied principally by Spath (1925), Seitz (1930), Brinkmann (1937), and Breistroffer (1947). To Brinkmann we owe a convincing demonstration of the origin of *Leymeriella* in the Desmoceratid *Callizoniceras*.

The present paper is an extract from a thesis on the Ammonoidea of the Lower Greensand formation of southern England prepared in the Geology Department of the University of Reading during a period of leave kindly granted the author by the Department of Scientific and Industrial Research. The nucleus of this extract is a systematic account of British occurrences of *Leymeriella*. Data obtained in the course of this research have led to conclusions of wider interest concerning the systematic position, distribution and ecology of the genus such as to justify advance publication.

[Palaeontology, Vol. 1, Part 1, 1957, pp. 28–59, pls. 7–10]

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Specimens collected in the course of the author's field work have been deposited in the Geological Survey Museum. The paper is published by permission of the Director of the Geological Survey of Great Britain.

MORPHOLOGY AND SYSTEMATIC POSITION OF *LEYMERIELLA*

As originally described by Jacob (1907, p. 368) *Leymeriella* was merely a subdivision of a broad genus *Hoplites* Neumayr, and the only taxonomic criteria mentioned were the single ribbing and simple suture-line. A fuller description was later published (Jacob 1908, p. 47) as follows:

> La coquille a des côtes généralement simples, peu flexueuses, interrompues par un sillon sur la région siphonale. La cloison, peu divisée, comporte un premier lobe latéral profond, symétrique; elle est surtout caractérisée par l'allure particulière de deux selles auxiliaires, qui forment un ensemble perpendiculaire à la suture ou même gagnant vers la bouche du côté de l'ombilic.

No type species was named and of the two species originally included in the genus by Jacob, namely *A. tardefurcatus* (Leymerie MS.) d'Orbigny and *Ammonites regularis* Bruguière, Spath (1925, p. 75) designated *A. tardefurcatus* as the type. Mme Basse (1952, p. 656) and Wright (1957, p. 392), however, cite *A. regularis* as the type, the latter author signifying that this type fixation was by original designation.

Seitz (1930) divided *Leymeriella* into two groups: (1) discoidal forms without tubercles on the flanks, such as *L. tardefurcata* (d'Orb.), *L. rencurelensis* (Jacob), *L. romani* (Jacob), *L. revili* (Jacob), and *L. hitzeli* (Jacob) and (2) more robust forms with both ventral and umbilico-lateral tubercles, typified by *L. regularis* (Brug.) and *L. pseudoregularis* Seitz. These two groups correspond roughly to two lineages of *Leymeriella* conceived by Brinkmann (1937) as having diverged from a common ancestry in the group of *L. schrammeni* at the base of the Tardefurcata Zone of the Lower Albian. The existence at the top of the Tardefurcata Zone of a host of species showing every gradation between the *tardefurcata* and *regularis* types suggests that Seitz and Brinkmann oversimplified the taxonomic and phylogenetic relationships within this 'genus'.

A more acceptable classification of *Leymeriella* and its allies was made by Breistroffer (1947). This author separated from *Leymeriella* s.s. the two subgenera *Proleymeriella* (for the group of '*Parahoplites*' *schrammeni* Jacob) and *Epileymeriella* (for the group of '*Parahoplites*' *hitzeli* Jacob). The former is an early development, untuberculated, and with ribs that sometimes branch on the flanks and which form chevrons on the venter. Its degree of morphological differentiation from *Leymeriella* is here considered sufficient to warrant full generic status. *Epileymeriella*, also without tubercles, is further characterized by the costae being unusually deeply and widely split, each branch tending to split again, so that double bifurcation is frequently produced.

Separation of *Leymeriella* as a distinct subfamily of the Hoplitidae was made independently by Breistroffer (1951, p. 266) and Wright (1952, p. 220), Breistroffer having priority. Later (1955, p. 571) Wright promoted it to family status within the Hoplitaceae on the grounds that its origin was too distinct to be included in the restricted Hoplitidae.

An important outcome of the present research is the recognition that *Leymeriella*, long classed with the Hoplitids, is a primitive member of the Lyelliceratidae. This family was created by Spath originally for the genera *Lyelliceras* Spath, *Neophlycticeras* Spath, and *Stoliczkaia* Neumayr, to which were subsequently added *Prolyelliceras* Spath, *Tegoceras* Hyatt (= *Rauliniceras* H. Douvillé), and *Budaiceras* Böse. It now comprises a host of Albian and basal Cenomanian genera, mostly unrepresented in Britain, and has been divided by Breistroffer (1953) into the two subfamilies Lyelliceratinae and Stoliczkainae. The last, being exclusively of Upper Albian and basal Cenomanian age, need not be considered further.

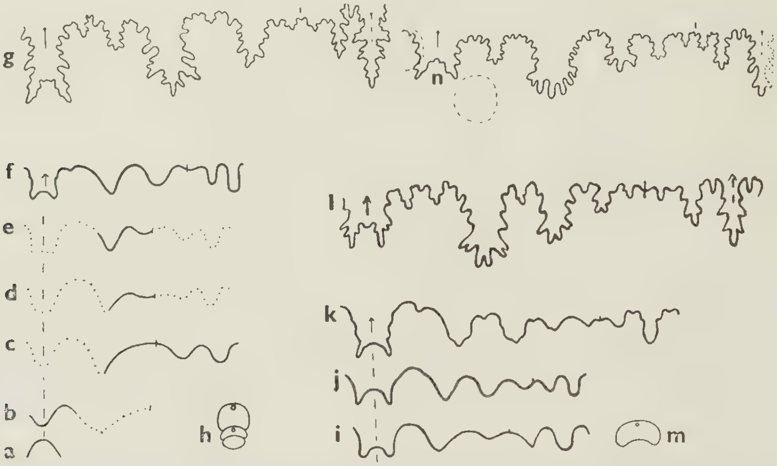
The family exhibits a diversity of morphological types and, as pointed out by Spath (1931, p. 313), while the siphonal row of tubercles is a distinctive feature of the Lyelliceratidae, yet some forms have the ventral aspect of *Hoplites* (i.e. a sulcate periphery) and others that of *Sonneratia* (i.e. an arched venter with strong costation continuous across the periphery).

Leymeriella as here interpreted encompasses a group of primitive Lyelliceratids that are characterized by loose coiling, shallow umbilicus, and venters of Hoplitid aspect. The suture-line is rather simple, with bifid saddles, a deep, parallel-sided ventral lobe and trifid lateral lobes, the auxiliaries showing little or no umbilical retraction. The whorls are generally compressed and of a basic subrectangular shape that may be modified to subhexagonal by the acquisition of ventral and umbilico-lateral tubercles. The ribs are uniform, straight or sigmoidal, and are generally flattened and grooved on the outer half of the whorl-side as though bifurcating. Near the umbilicus the ribs may be pinched up into a flare or may bear a distinct spinose tubercle; their ventral terminations usually form clavi bordering a median ventral sulcation, each clavus placed in line with its fellow on the opposite side of the venter. The umbilical wall is seldom steeply sloped and has no definite rim. Widening of the umbilicus, loss of tuberculation, and crowding of the ribbing are features of maturity. 'Gerontic' specimens may exhibit constrictions and ventral ribs that unite in the form of chevrons. The body-chamber occupies about half a whorl and terminates in a plain mouth-border.

Grounds for transferring *Leymeriella* to the Lyelliceratidae may be stated as follows:

Coiling. Ignoring the immediate post-embryonic whorls, in which, as in most ammonites, there is a rapid change in geometric relations, the shell of *Leymeriella* forms a slowly unwinding spiral. The degree of overlap of the whorls is never very profound and decreases with age until, at say 70–80 mm. diameter, the whorls are merely in contact, only the ventral tubercles leaving an impression on the dorsum of the last whorl. This condition of coiling is paralleled in *Lyelliceras* and *Prolyelliceras*. In the Hoplitidae, which grow to a much larger size, relatively tight coiling and a well-impressed dorsum are maintained through life.

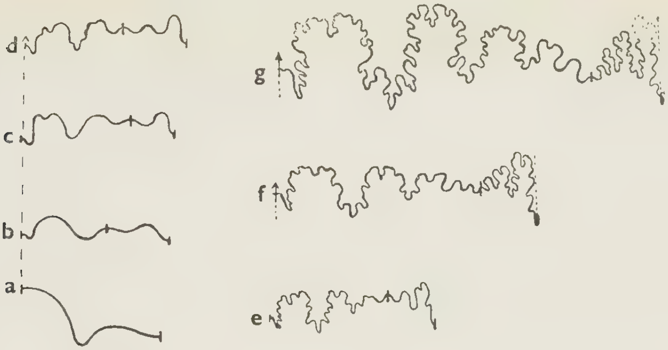
Suture-line. The ontogenetic development of the suture-line of *Leymeriella* has been worked out by dissection of immature specimens of *L. consueta* sp. nov. of the Regularis Subzone and is illustrated in text-fig. 1. The first suture-line, *a*, may be assumed to be of the angustisellate type common to the embryonal stage of all post-Triassic ammonites, though only the high external saddle could be made out. It will be observed that the second and third sutures, *b* and *c*, possess a shallow ventral lobe and two broad saddles that are separated by a deep, V-shaped lateral lobe; internally a well-developed umbilical lobe is already present adjacent to the antisiphonal lobe. In subsequent growth stages, *d* and *e*, the second lateral lobe originates as an embayment of the broad lateral saddle and is later pushed outwards up the flank as the second lateral saddle ripples out from the umbilical seam. By the second whorl, *f*, when the ammonite is still less than 2 mm. diameter, the elements of the adult suture-line have been laid down and there is no further development beyond minute elaboration of this basic pattern. Shortening of the internal suture-line, accompanied by some degree of atrophy of the umbilical lobe, is a mechanical adjustment to the rapid change in whorl-shape from cadicone to subrectangular, strikingly exhibited in the first two volutions (text-fig. 1*h*). Thus the sutural development of *Leymeriella* takes place mainly on the external side, the internal portion retaining throughout ontogeny only the elements present in the primitive suture-line. This contrasts sharply with the growth of sutural characters in the Hoplitidae (text-fig. 2), but is



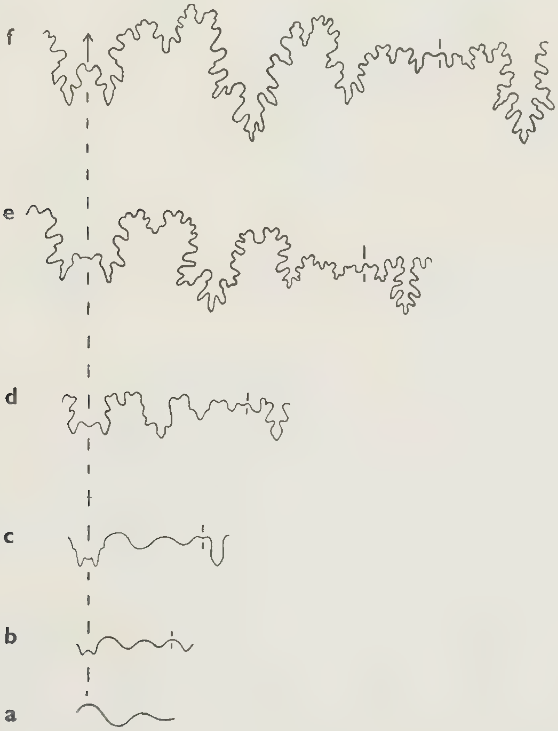
TEXT-FIG. 1. Suture-lines and early whorls of Lyelliceratidae. *a–h*, *Leymeriella* (*Leymeriella*) *consueta* sp. nov. *a*, *b*, *c*, *d*, *e* = 1st, 2nd, 3rd, 9th, and 12th sutures; *f* = suture-line at 1·75 mm. diameter; *h* = protoconch and first two whorls. W.W. 8410, Regularis Subzone (Band I), Arnold's Pit, Leighton Buzzard, Beds.; *g* = suture-line at *c.* 45 mm. diameter, enlarged ×2·5. Locality and horizon as before. Author's Coll., G.S.M. Zm 2024.

i–m, *Lyelliceras lyelli* (d'Orbigny). *i*, *j*, *k* = suture-lines at 1·5, 2, and 4 mm. diameter; *m* = whorl-section at 1·5 mm. diameter. F. G. H. Price Coll., G.S.M. FOR. 58, Middle Albian (Dentatus Zone), Gaty, France; *l* = suture-line at 20 mm. diameter. Locality, horizon, and collector as before. G.S.M. FOR. 57.

n, *Tegoceras gladiator* (Bayle). Complete suture-line at 40 mm. diameter. Author's Coll., G.S.M. Zm 2023, Mammillatum Zone, Ford Place, Wrotham, Kent.



TEXT-FIG. 2. Suture-line development of a Hoplitid ammonite. *a*, *b* = 1st and 2nd sutures; *c*, *d*, *e*, *f*, *g* = suture-lines at 2·5, 4, 5, 8, and 17 mm. diameter; *f* and *g* based on specimens of '*Hoplites auritus*' (Price *non* J. Sowerby) from the Middle Gault of Dunton Green, Kent. After Spath, Monograph of Gault Ammonites, text-fig. 1.



TEXT-FIG. 3. Suture-line development of *Deshayesites deshayesi* (Leymerie MS.) d'Orbigny sp. *a*, *b* = 1st and 2nd sutures, from a topotype in the Sorbonne Coll., Lower Aptian (Deshayesi Zone), Bailly-aux-Forges (Haute-Marne); *c*, *d*, *e* = suture-lines at 2, 8, and 16 mm. diameter; same horizon and collection, St. Dizier (Haute-Marne); *f* = suture-line at 34 mm. diameter; horizon, locality, and collection as for *a*, *b*.

normal for the Lyelliceratidae, as I have ascertained by study of juvenile specimens of *Lyelliceras*. It is only necessary to compare the external suture-lines of *Leymeriella* with those of *Lyelliceras* as figured by d'Orbigny (1841, pl. 74, fig. 6) and Pictet and Campiche (1859, pl. 24, figs. 6*c*, 9) to appreciate the essential similarities, especially in the almost radial course of the septal edge across the flank. These similarities are enhanced when comparison is made with the complete suture-line of *Lyelliceras* or *Tegoceras* (text-fig. 1, *i–n*). In the retardation of development of the internal portion of the suture-line the Lyelliceratidae recall the Deshayesitidae of the Aptian (text-fig. 3) rather than the Hoplitidae. In the last family the septal edge has a strong umbilical retraction and the suture-line is folded into numerous lobes and saddles on both sides of the umbilical seam.

Sculpture. No Hoplitid ammonite possesses the single, uniform ribbing of *Leymeriella*; such ribbing is altogether typical of the early Lyelliceratidae, *Lyelliceras*, *Prolyelliceras*, and *Tegoceras*. Compare, for instance, the lateral aspect of *Leymeriella rudis* sp. nov. (Pl. 8, fig. 6) and *Tegoceras gladiator* (Bayle) (Pl. 7, fig. 8) or of the species of *Leymeriella* and *Prolyelliceras* illustrated in Pl. 7. Umbilico-lateral tuberculation arises in *Leymeriella* from the pinching up of the ribs near the umbilicus; this structure is strictly homologous with the lateral bulge of the ribs in *T. gladiator* and is quite different from the bullate tubercles found in the Hoplitidae. The paired ventral clavi of *Leymeriella* offer a strong similarity to those of the Hoplitidae. Here again, this genus merely carries to extremes a tendency manifest in *T. gladiator*, the zigzag ventral ribbing of which simulates that of its Hoplitid contemporary *Otohoplites*.

EXPLANATION OF PLATE 7

Figs. 1, 1*a–c*. *Pseudoleymeriella haidaquensis* (Whiteaves), Lower Albian (Haida Formation), Skidegate Inlet, Queen Charlotte Islands. Plaster cast of holotype (1, 1*a*) with suture-line, enlarged ×4 (1*b*) and whorl-section (1*c*). Geol. Surv. Canada 5991.

Figs. 2, 2*a*. *Proleymeriella schrammeni* (Jacob), Tardefurcata Zone (Schrammeni Subzone), Algermissen, Hanover. Topotype. B.M. C. 14398; A. Schrammen Coll.

Figs. 3, 3*a*. *Proleymeriella phoenix* sp. nov. Locality and horizon as for Fig. 2. B.M. C. 14397; A. Schrammen Coll.

Figs. 4, 4*a*. *Callizoniceras* (*Wollemanniceras*) *keilhacki* (Wollemann), Upper Aptian, Nodosocostatum Zone (Jacobi Subzone), Schwiecheldt, Hanover. W.W. G 831.

Fig. 5. *Callizoniceras* (*Wollemanniceras*) *keilhacki* (Wollemann), Upper Aptian, Nodosocostatum Zone (Jacobi Subzone), Algermissen, Hanover. Copy of Wollemann 1904, pl. 5, fig. 5.

Fig. 6. *Prolyelliceras* sp., transitional to *Brancoceras*, condensed Lower–Middle Albian, Pielle (Alpes Maritimes). W.W. F 1, ×2.

Figs. 7, 7*a*. *Proleymeriella schrammeni* (Jacob), Tardefurcata Zone (Schrammeni Subzone), Schwiecheldt, Hanover. Side view and whorl-section of nucleus. W.W. G 821, ×2.

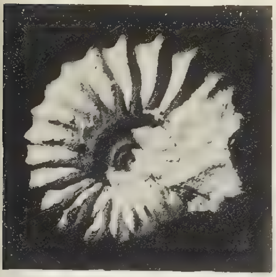
Figs. 8, 8*a*. *Tegoceras gladiator* (Bayle). Locality and horizon as for Fig. 6. Side view and whorl-section. W.W. F 2.

Fig. 9. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp., condensed Lower–Middle Albian of Près de Rencurel (Isère). Copy of Jacob 1908, pl. vii, fig. 12*a*.

Fig. 10. *Leymeriella* (*Leymeriella*) *rudis* sp. nov., Lower Greensand, Tardefurcata Zone (Regularis Subzone), Band I, Arnold's Pit, Leighton Buzzard, Beds. Plasticine impression of a natural mould. W.W. 20547.

Fig. 11. *Proleymeriella* sp. aff. *gevreyi* (Jacob), Gault, Middle Albian, Dentatus Zone, Dienville (Aube). G.S.M. FOR 65; F. G. H. Price Coll.

Fig. 12, 12*a*. *Eubrancoceras* sp., Gault, Middle Albian, Dentatus Zone (Dentatus-spathi Subzone), Colley Lane Pit, Reigate, Surrey. R. A. Beaney Coll.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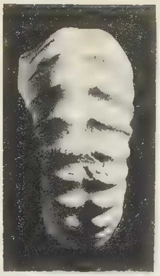
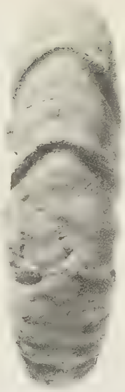
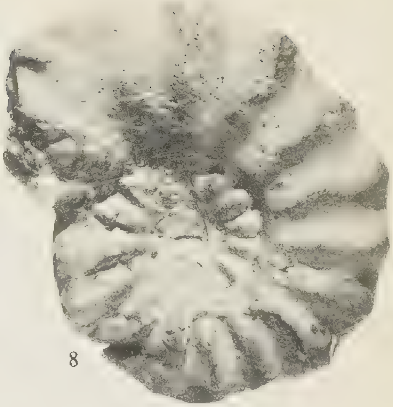

1*a*


4*a*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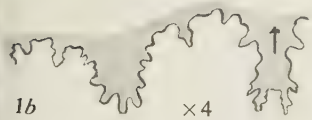
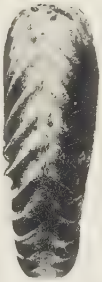
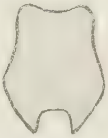
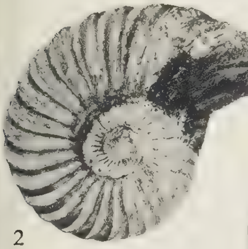

1*b* ×4


2*a*


8*a*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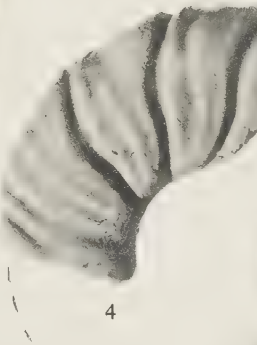
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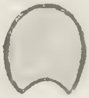
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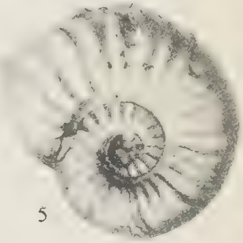
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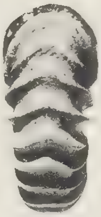
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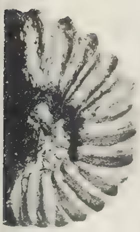
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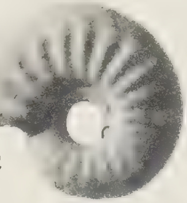
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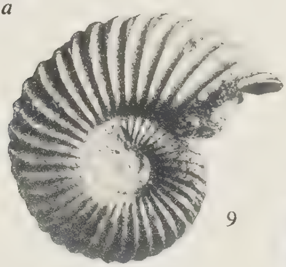
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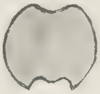
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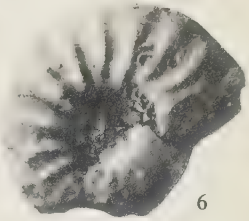
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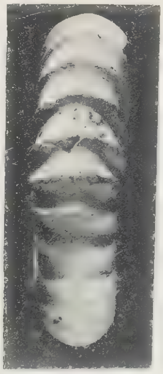
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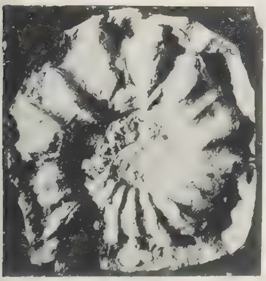
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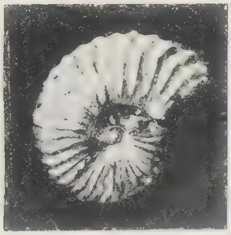
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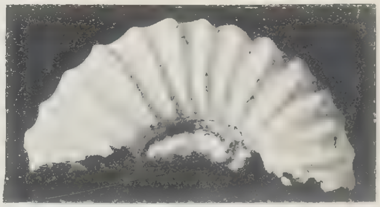
12*a*

CASEY, Early Acanthocerataceae

Turning now to the wider field of Albian Acanthocerataceae, we may note other morphological parallels that give support for the inclusion of the Leymeriellinae in this superfamily. Reference may first be made to the likeness of *Proleymeriella* and the Brancoceratidae, a family that is intimately connected with the Lyelliceratidae and the Mojsisovicsiidae. On Pl. 7, figs. 3, 3*a* is illustrated an inflated development of *Proleymeriella*, *P. phoenix* sp. nov., that differs from *P. lemoinei* (Jacob) in its coarser, less flexuous, and sharper ribbing, the ribs being rarely divided and strongly elevated on the venter. But for the high relief and chevron-like extension of the ventral costation this species might have passed for a *Eubrancoceras*; and it is interesting to observe that a species of *Eubrancoceras*, similar to that illustrated on Pl. 7, figs. 12, 12*a*, has been figured from Peru by Steinmann (1929, p. 123, fig. 134) as *Parahoplites* aff. *schrammeni* Jacob. On the same plate I am figuring the early whorls of *P. schrammeni* and of a *Brancoceras-Prolyelliceras* hybrid for comparison with those of *Lyelliceras ulrichi* Knetchel, illustrated by Benavides-Cáceres (1956, pl. 51, figs. 6–7). The fact that they are all strikingly similar to *Callizoniceras keilhacki* (Wollemann) (Pl. 7, fig. 5), the ancestor of *P. schrammeni*, and are easily separable from juvenile Hoplitidae is at once apparent.

Another important link between the Brancoceratid-Lyelliceratid complex and the Leymeriellinae is provided by *Pseudoleymeriella* gen. nov., at present known only by its type species, *Hoplites haidaquensis* Whiteaves (holotype the original of Whiteaves 1893, p. 444, pl. 7, figs. 2, 2*a–b*) from the Lower Albian (Haida Formation) of the Queen Charlotte Islands, and refigured in Pl. 7, figs. 1, 1*a–c*. This differs from all species of *Leymeriella* in its subcircular whorl-section, in the absence of flattening or grooving of the costae, and in not having the terminations of the ribs on each side of the ventral sulcus elevated into forwardly directed clavi. The suture-line is rather simple and combines the deep, narrow ventral lobe of *Leymeriella* with a broad, open first lateral lobe. Breistroffer (1947, p. 70) has commented on the resemblance of the ornament of *Leymeriella crassa* Spath to that of *Mojsisovicsia spinulosa* (Spath). Concerning links with the Mojsisovicsiidae, it may further be noted that the flattening of the costae on the outer part of the flank, one of the most characteristic features of *Leymeriella*, is reproduced in *Mojsisovicsia*, *Oxytropidoceras*, and other primitive members of that family, as well as in *Brancoceras*. *Mojsisovicsia delaruei* (d'Orbigny), of the Middle Albian, at 10 mm. diameter has the same style of costation as immature *Leymeriella tardefurcata*. Grooving of these flattened costae is not a feature of the Mojsisovicsiidae or the Brancoceratidae, it is true. Observe, therefore, the reappearance of grooved and flattened ribs in *Neokentroceras*, an Upper Albian derivative of the Brancoceratidae (see Spath 1921, p. 141, text-fig. D 1, *N. curvicornu*). Remove the keel of *Neokentroceras speciosum* Haas (1942, pl. 8, fig. 14) and we have a life-size morphic equivalent of the adolescent *Leymeriella consueta* var. *magna*, complete with subhexagonal whorl-section, horn-like outer tubercles, and coarse, widely-spaced ribs. It will be unnecessary to labour the point further: the specimens speak for themselves.

It is now suggested that three subfamilies should be recognized in the Lyelliceratidae: (1) Leymeriellinae Breistroffer, exclusively of Lower Albian age, (2) Lyelliceratinae, ranging from Lower to Middle Albian, and (3) Stoliczkainae Breistroffer, of Upper Albian and basal Cenomanian age.

LEYMERIELLA AND THE ORIGIN OF THE ACANTHOCERATACEAE

The case for assimilating the Leymeriellinae to the Lyelliceratidae has been presented above; here it is pertinent to observe that the Lyelliceratidae, appearing in the Lower Albian, are the direct forerunners of the Cenomanian Acanthoceratidae and that they are acknowledged to constitute the main stem from which the superfamily Acanthocerataceae developed. The origin of the Lyelliceratidae themselves is more obscure. Reviewing this family in his Monograph of the Gault Ammonoidea, Spath (1931, p. 314) emphasized the probability of a common origin of the Lyelliceratidae, Mojsisovicsiidae, and the Brancoceratidae, *Brancoceras* being considered closest to the ancestral stock. This ancestral stock was thought to belong most likely to the Parahoplitidae, a view expressed by Spath on a previous occasion (Spath 1922, pp. 108–9) and, before him, by Jacob (1907, p. 361). In the concluding chapters of his Monograph, however, the idea of descent from the Parahoplitidae was abandoned, the discovery of Brancoceratidae with *Silesitoides*-like inner whorls suggesting a more direct liaison with the Desmocerataceae (Spath 1942, p. 710). New collections from the Albian of many parts of the world, but especially from south-east France (e.g. a collection from the Peille (Alpes Maritimes) neighbourhood, made available to me through the good offices of Mr. C. W. Wright), have brought to light so many transitional types between the Lyelliceratidae, Mojsisovicsiidae and the Brancoceratidae, as to leave no room for doubt that these three families are parts of a single genetic complex. For the source of this complex we must examine the clues offered by *Leymeriella*.

Leymeriella is one of the few trachyostracous genera for which there is convincing evidence of ancestry in the Desmocerataceae, the feebly ornamented, long-lived stock which is the theoretical evolutionary reservoir of so many Cretaceous ammonites. Thanks to the work of Brinkmann (1937), referred to above, *Leymeriella* may be traced back to the Desmoceratid *Callizoniceras*. Bed by bed collecting from the uniform suc-

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EXPLANATION OF PLATE 8

Figs. 1–3. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp., condensed Regularis-Mammillatum bed of the Ardennes and Meuse Departments of France. 1, 3, 3*a*, two examples leading to var. *intermedia* Spath, from Novion, near Machéroménil (Ardennes) (Muséum d'Histoire Naturelle, Paris; d'Orbigny Coll.). 2, 2*a*, a septate nucleus from Varennes (Meuse) (École des Mines, Paris; Raulin Coll.).

Figs. 4, 4*a*. *Leymeriella* (*Leymeriella*) aff. *consueta* sp. nov., transitional to *L.* (*L.*) *renascens* Seitz, condensed Regularis-Mammillatum bed, Novion, near Machéroménil (Ardennes) (Muséum d'Histoire Naturelle, Paris; d'Orbigny Coll.).

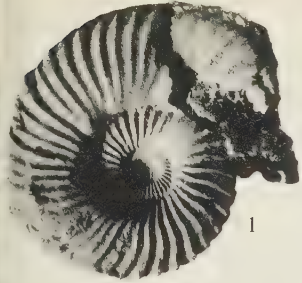
Figs. 5, 5*a–b*. *Leymeriella* (*Leymeriella*) *regularis* (Bruguière) d'Orbigny. Same horizon, Sauces, near Machéroménil (Ardennes). Neotype. Side view (5), ventral view (5*a*), and restored whorl-section (5*c*) (École des Mines, Paris; Raulin Coll.).

Figs. 6, 6*a–b*. *Leymeriella* (*Leymeriella*) *rudis* sp. nov. Side view (6), and front view (6*a*) of holotype, with whorl-section (6*b*) of another specimen. Locality and horizon as for Fig. 4 (Muséum d'Histoire Naturelle, Paris; d'Orbigny Coll.).

Fig. 7. *Leymeriella* (*Leymeriella*) *consueta* var. *magna* nov., nucleus. Locality, horizon, and collection as for Fig. 4.

Figs. 8, 8*a*. *Ammonites tardefurcatus* (Leymerie MS.) d'Orbigny, from the Albian of the Aube. Copy of d'Orbigny 1841, pl. 71, figs. 4, 5, slightly reduced.

Figs. 9, 9*a–b*. *Ammonites regularis* (Bruguière) d'Orbigny, from the Albian of the Machéroménil district. Copy of d'Orbigny 1841, pl. 71, figs. 1, 2, 3, slightly reduced.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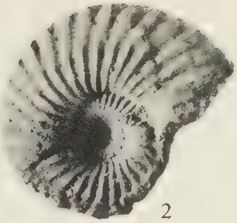
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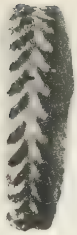
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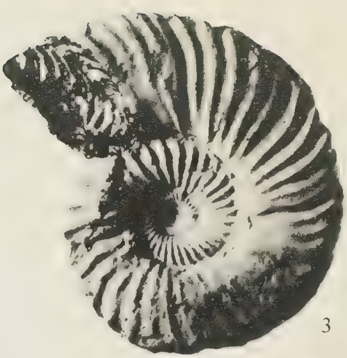
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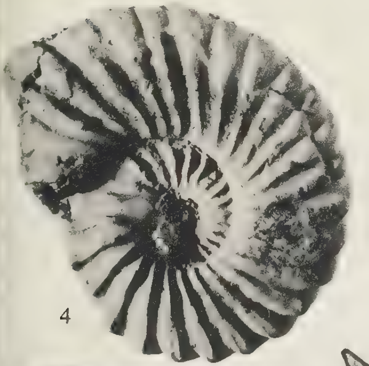
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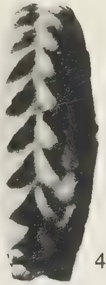
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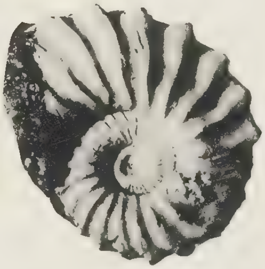
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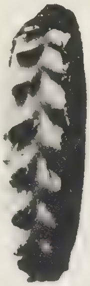
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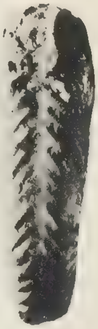
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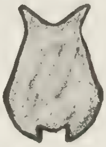
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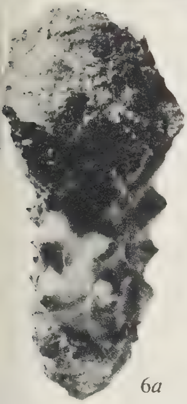
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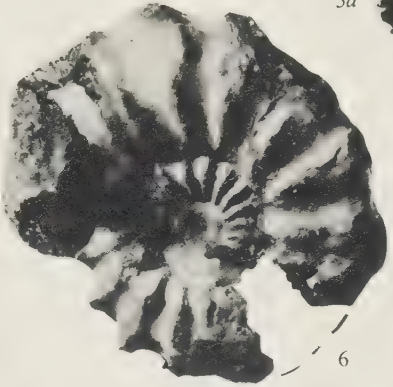
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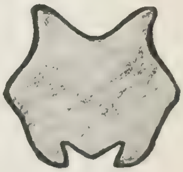
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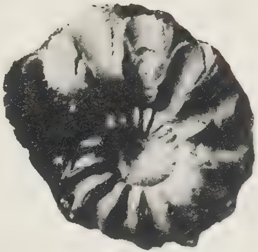
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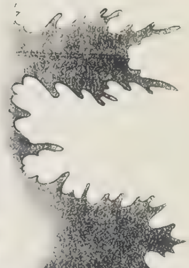
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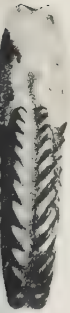
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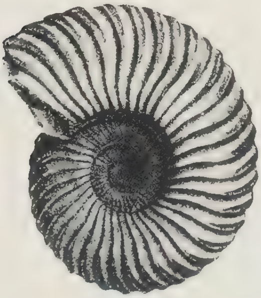
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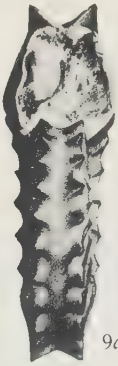
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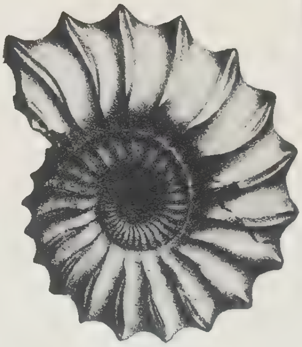
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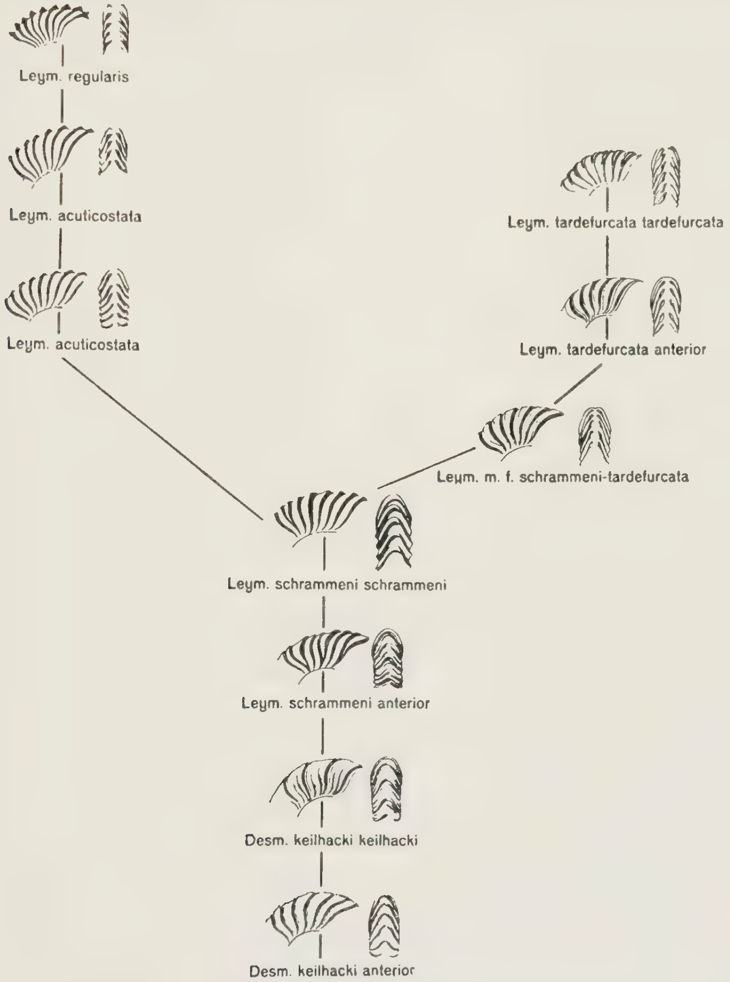
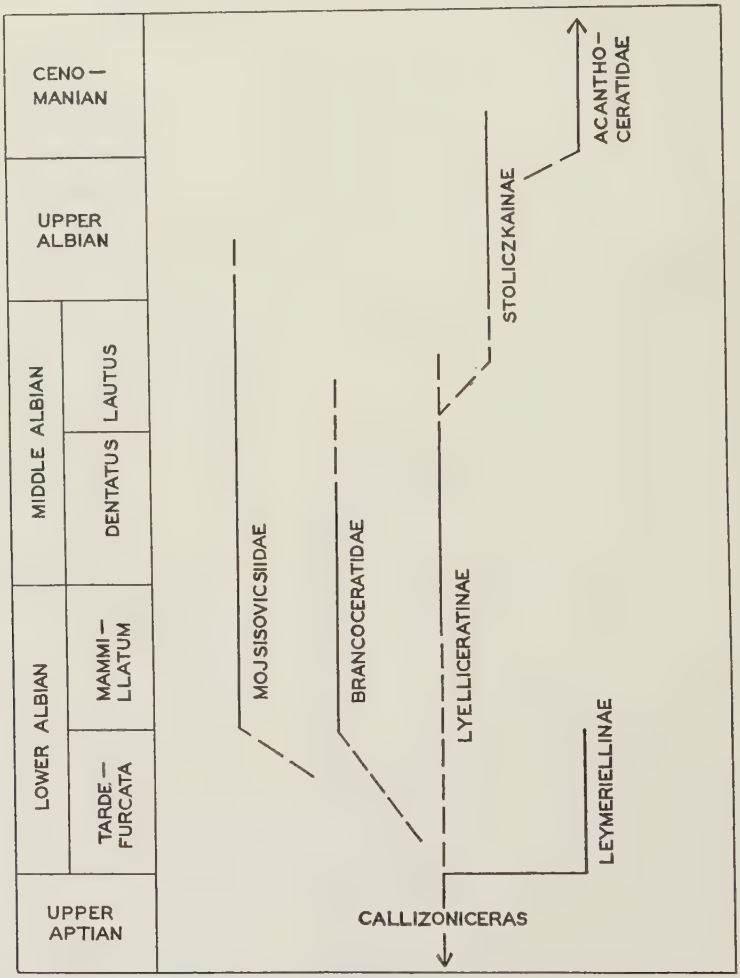
CASEY, *Leymeriella* from France

ession of clays that constitute the Upper Aptian and Lower Albian of north Germany rovided Brinkmann with a suite of specimens that show a gradual passage upwards rom *Callizoniceras* (*Wollemanniceras*) *keilhacki* (Wollemann) of the Jacobi Subzone


Leym. regularis
Leym. acuticostata
Leym. acuticostata
Leym. tardefurcata tardefurcata
Leym. tardefurcata anterior
Leym. m. f. schrammeni-tardefurcata
Leym. schrammeni schrammeni
Leym. schrammeni anterior
Desm. keilhacki keilhacki
Desm. keilhacki anterior

TEXT-FIG. 4. Evolution of *Leymeriella* from the Desmoceratid *Callizoniceras*. Copy of Brinkmann 1937, text-fig. 4, p. 6. (For *Desm. keilhacki* read *Callizoniceras keilhacki*; for *Leym. schrammeni* read *Proleymeriella schrammeni*; for *Leym. tardefurcata anterior* read *Leymeriella* (*L.*) *germanica* sp. nov.)

rough *Proleymeriella schrammeni* (Jacob) and allies to the typical *Leymeriella* (text-g. 4). This transformation was achieved by first, the acquisition of strong ribbing, fol-wed by flattening of the ribs and the appearance of a ventral groove, and finally, ooving and tuberculation of the ribs. Discovery of 'gerontic' specimens of *Leymeriella* the Lower Greensand indicates that the evolution of the genus followed the principle proterogenesis; if growth proceeded long enough the ammonite returned to a *Proley-* *eriella* or a *Callizoniceras* condition. Jacob (1908) had already indicated *P. schrammeni* as the point of origin of *Leymeriella*, but his association of this species with the Aptian Parahoplitidae was ill conceived, as also was Roman's derivation of *Leymeriella* from the Douvilleiceratidae (Roman 1938, p. 360). Brinkmann's results, readily confirmed by a series of duplicate specimens collected in north Germany by Mr. E. V. Wright and kindly passed to the author for study, take on a new significance in the light of the relationship of *Leymeriella* to *Lyelliceras* and its membership in the Acanthocerataceae. It now seems fair to assume as a working hypothesis that the Lyelliceratidae (including Leymeriellinae), Brancoceratidae, and Mojsisovicsiidae were simultaneous and rapidly differentiating offshoots of a small group of Desmoceratidae centred around *Callizoniceras*. Spath's view as to the common origin of the early Acanthocerataceae and their evolution in the Lower Albian from the Desmoceratidae is thus given strong support, except that emphasis is now placed on *Callizoniceras* rather than *Silesitoides* as the ancestral source. The stratigraphical distribution and probable interrelations of the

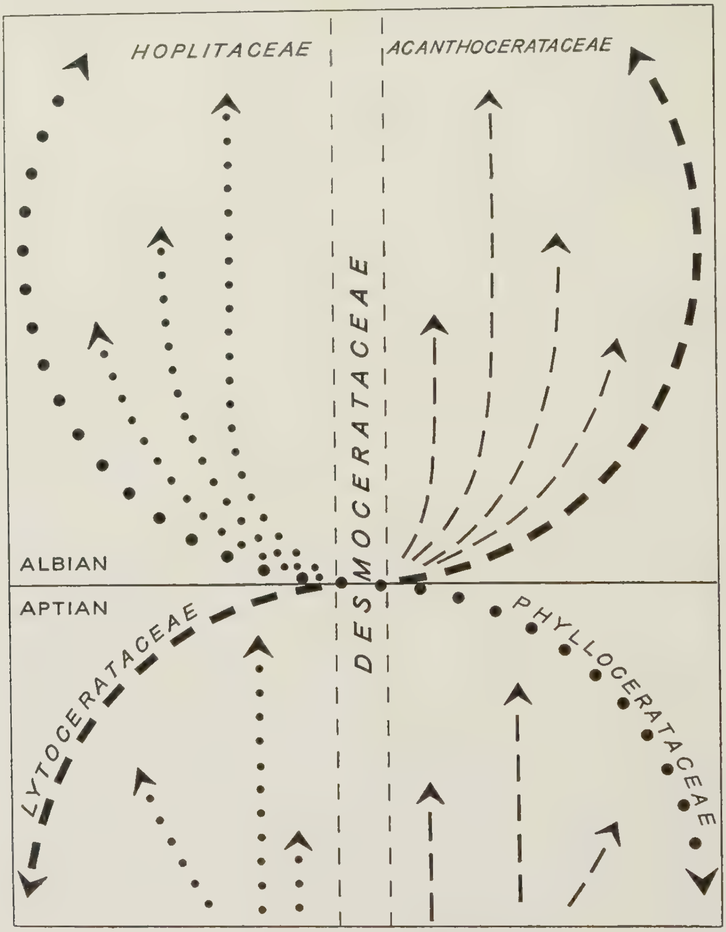


TEXT-FIG. 5. Probable interrelations of early Acanthocerataceae.

family units discussed herein are illustrated diagrammatically in text-fig. 5. Owing to the imperfection of the European record in Lower Albian times, the views here put forward must await confirmation and amplification from other regions.

Evidence of eruptive evolution, expressed in numerous adaptive radiations from a single point of origin, is not confined among Albian ammonites to the Acanthocerataceae. The trend of research during recent years has been to narrow down the ancestral stock of the Hoplitidae (including Cleoniceratinae) to the Desmoceratid *Uhligella*. Simultaneous with the appearance of *Proleymeriella* at the base of the Tardefurcata Zone is the entry of several branches of the Hoplitinae and Cleoniceratinae showing affiliation to *Uhligella*, notably the genus *Farnhamia* Casey. And it is believed that later Hoplitid genera sprang from these early Tardefurcata Zone prototypes and do not represent successive waves of ornamented Desmoceratids (cf. Casey 1954, p. 107; Wright 1955, p. 571). Apart from genera surviving from the Aptian, it is now possible to visualize the trachyostracous ammonoidea of the Albian as the product of two independent but synchronous radiations from the Desmocerataceae; one from *Callizoniceras* (Acanthocerataceae), leading via Lyelliceratidae to the Acanthoceratidae; the other from *Uhligella* (Hoplitaceae), giving rise to the Hoplitidae and thence the Schloenbachiidae and Forbesiceratidae. The Desmocerataceae were regarded by Spath as a polyphyletic assemblage of derivatives of both Lytocerataceae and Phyllocerataceae, the two fundamental post-Triassic ammonite stocks (Spath 1923, p. 33), a view shared by the present author, though not by all workers (e.g. Wright 1955). *Callizoniceras* has been claimed as a *Lytoceras* derivative (Salfeld 1924), while *Uhligella* is intimately linked with *Beudanticeras*, which, via forms like *B.* (‘*Pseudorbulites*’) *convergens* (Jacob) (= *Uhligella convergens* Jacob), shows a passage into the Phylloceratidae. If these affiliations are correctly assessed they carry great implications in the field of ammonite phylogeny, for the picture that now emerges is of an evolutionary stimulus at the commencement of the Albian giving rise to a co-ordinated burst of activity from both the Phylloceratidae and the Lytoceratidae. On the one hand, the Phylloceratid derivatives (Hoplitaceae) retain tight coiling and a suture-line with retracted serial auxiliaries; on the other, the Lytoceratid offshoots (Acanthocerataceae) betray their origin in their more evolute coiling and simpler suture-line, sometimes (as in adult *Lyelliceras*) with the ancestral bifurcation of the lateral lobes. Text-fig. 6 attempts to illustrate these phylogenetic speculations in diagrammatic form.

It is not proposed on this occasion to discuss fully the various Aptian and Neocomian families that have been at one time or another placed in the Acanthocerataceae (e.g. Douvilleiceratidae, Pulchelliidae) and now, together with Parahoplitidae and Deshayesitidae, grouped into a heterogeneous ‘Hoplitaceae’ (Wright 1955, 1957). Unpublished investigation of the Aptian families has shown that they too constitute at least two separate radiations, distinct both from each other and from later radiations in the Albian, though in the case of the Deshayesitidae following a similar course of evolution to that of the Lyelliceratidae. Thus the Deshayesitidae, also springing from *Callizoniceras*, have a *Proleymeriella* phase (*Deshayesites*) and a *Leymeriella* phase (*Dufrenoyia*), and produce multituberculated offshoots (*Cloioceras*, *Somalites*), the latter a homoeomorph of *Lyelliceras*. If the pseudoceratitic developments of the Albian and Upper Cretaceous (Engonoceratidae and Placenticeratidae) are indeed the final expression of this Deshayesitid lineage, as has been frequently suggested (just as the Sphenodiscidae are the pseudoceratitic end-forms of the Acanthoceratacae), it may be necessary to revive for it Hyatt's superfamily name Placenticeratacae (Hyatt 1900, p. 584; published as Placenticeratida).



TEXT-FIG. 6. Hypothetical origin of the Hoplitaceae and Acanthoceratacae in Phylloceratacae and Lytoceratacae respectively, both via the Desmoceratacae.

DISTRIBUTION OF THE LEYMERIELLINAE AND THE ZONAL CLASSIFICATION OF THE LOWER ALBIAN

The Leymeriellinae belong typically to the Northern Hemisphere and are found in deposits of Tardefurcata age that extend from the Urals across Europe westwards to the east coast of Greenland. Penetration to the Equatorial Region, where the Lyelliceratinae, Brancoceratidae, and Mojsisovicsiidae found a congenial habitat, does not seem to have taken place. Records of *Proleymeriella* (*schrammeni* group) from South America (Steinmann 1929, p. 123; Gerth 1935, p. 362) are based on misidentified Brancoceratidae, while the supposed occurrence of *Leymeriella* in Zululand (Haughton 1936, pp. 292–7) is not supported by illustrations and must be accepted with reservation. Imlay and Reeside's reference to *Leymeriella* in the Queen Charlotte Islands (Imlay and Reeside 1954, p. 230) relate to *Pseudoleymeriella haidaquensis* (Whiteaves).

Occurrences of Leymeriellinae are intimately bound up with the zonal classification of the Lower Albian. Stratigraphers and palaeontologists are not agreed, however, as to the limits of the Lower Albian or as to its zonal subdivisions. In the present paper the Lower Albian substage is given the interpretation placed upon it by Breistroffer (1947) and comprises two zones, *Leymeriella tardefurcata* below and *Douvilleiceras mammillatum* above. The use of *L. tardefurcata* as a zonal index is of long standing and dates at least from von Strombeck (1856).

It is only in north Germany that the vertical distribution of the Leymeriellinae can be followed with any approach to continuity; elsewhere, as in Britain, the record is incomplete, or, as in France, is difficult to decipher owing to condensed deposition. Brinkmann (1937), improving upon the earlier scheme of Stolley (1908), proposed the following classification of the German *Leymeriella* and *Proleymeriella* horizons:

Zones	Subzones
Leymeriella regularis	*Hoplites spp.*
	L. hitzeli
Leymeriella tardefurcata	*L. tardefurcata tardefurcata*
	L. tardefurcata anterior
Leymeriella schrammeni	*L. schrammeni schrammeni*
	L. schrammeni anterior

This classification was emended and simplified by Spath (1942) to conform to the scale of subdivision employed in his comprehensive Albian zonal table. Spath retained a single broad zone of *L. tardefurcata* and recognized three subzones only, in ascending order, *L. schrammeni*, *L. acuticostata*, and *L. regularis*. *L. acuticostata* Brinkmann was chosen as a substitute for Brinkmann's subspecies of *L. tardefurcata* to avoid the use of *L. tardefurcata* both as a zonal and a subzonal fossil.

It must be strongly emphasized that these detailed subdivisions are at present applicable only to north Germany. Outside this area it is only in the topmost part of the Tardefurcata Zone, immediately underlying the Mammillatum Zone, that *Leymeriella* is abundant and widespread. For this part of the succession von Strombeck (1856), Stolley (1908), Spath (1923, 1942), and Brinkmann (1937) all use *L. regularis* as the guide fossil. The term 'Regularis Subzone' for this horizon has become commonplace in British literature. In 1947, however, Breistroffer (1947, pp. 24, 54) proposed to replace *L. regularis* as an index fossil by *L. canteriata* (Defrance) Brongniart sp., the latter being regarded as a senior synonym of *L. pseudoregularis* Seitz. According to this authority, in the Machéroménil district (Ardennes), whence came d'Orbigny's specimens, *L. regularis* is a rare form of the Mammillatum Zone and it is doubtful if it occurs at all in earlier strata. When discussing the faunal sequence of the Lower Albian in general, Breistroffer appears to discredit all records of *L. regularis* from below the Mammillatum Zone and to assume that they refer to *L. canteriata* (= *pseudoregularis*). In 1950 I pointed out (Casey 1950, p. 293) that whatever the zonal origin of d'Orbigny's specimens, there is adequate evidence to show that in England at least both *L. pseudoregularis* and a form indistinguishable from *L. regularis* as figured by d'Orbigny occur side by side *below* the Mammillatum Zone and that no change in zonal nomenclature is required. Further investigation of this anomalous record of *L. regularis* in the Mammillatum Zone discloses that there is in fact no discrepancy of horizon between the English and French occurrences of *L. regularis*. The apparent discrepancy is due to the failure of French palaeontologists to realize that the Machéroménil fauna, though contained in a single band of phosphatic nodules (Barrois 1878), is condensed and includes not only elements of many different horizons of the Mammillatum Zone but also of the Regularis Subzone of the Tardefurcata Zone. The reasons for this view are as follows:

1. Despite intensive collecting, not a single specimen of *Leymeriella* has been found in the Mammillatum Zone of Kent, where this zone is uncontaminated by fossils derived from the Tardefurcata Zone, though it has yielded every other ammonite genus known in the Mammillatum Zone of Europe, even such exotic genera as *Parengonoceras*, *Tegoceras*, *Uhligella*, and *Oxytropidoceras*.
2. *Leymeriella* is well represented in the Machéroménil assemblage. *Leymeriella regularis*, *L. tardefurcata* (with its var. *intermedia*), *L. consueta* (with its var. *magna*), and *L. rudis* are all present in the collections from this nodule-bed in the Paris Museums. These collections support Barrois's record of *L. regularis* as a common fossil at Machéroménil.
3. Every species and variety of *Leymeriella* found in the 'Mammillatum' nodule-bed of the Ardennes and Meuse Departments of France is found in the Regularis Subzone of southern England.
4. Some of these Machéroménil *Leymeriella* have impressions of other *Leymeriella* in the matrix (see Pl. 8, fig. 3), indicating that they were obtained from 'graveyard' nodules similar to those in the English Regularis Subzone. In no case did I find a Machéroménil *Leymeriella* in the same nodule as a Mammillatum Zone ammonite.

The occurrence of *L. regularis* with Mammillatum Zone ammonites at Machéroménil is thus strictly comparable with its occurrence in Band II at Leighton Buzzard, Beds. (Wright and Wright 1947), or in Bed 7 of Chalvington, Sussex (Casey 1950, p. 276). It

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EXPLANATION OF PLATE 9

Figs. 1, 1*a*. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny, *s.l.* Adult body-chamber showing *Proleymeriella* type of ventral ribbing. Regularis Subzone (Bed 5), Wrecclesham, Surrey. G.S.M. Zm 1309; author's Coll.

Fig. 2. *Leymeriella* (*Leymeriella*) *regularis* (Bruguière) d'Orbigny, condensed Regularis-Mammillatum beds (exact bed unknown), Arnold's Pit, Leighton Buzzard, Beds. B.M. C 40348; G. W. Coles Coll.

Figs. 3, 3*a*. *Leymeriella* (*Leymeriella*) cf. *renascens* Seitz. Locality, horizon, and collector as for Fig. 2. B.M. C. 36627.

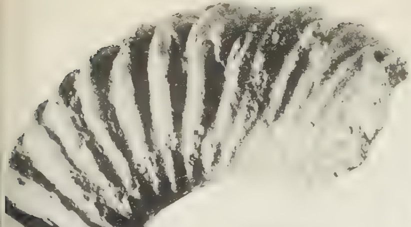
Figs. 4, 4*a*. *Leymeriella* (*Leymeriella*) *consueta* var. *magna* nov. Side view (4), with whorl-section taken at point indicated by *x* (4*a*) of type of variety. Locality and horizon as for Fig. 1. W.W. 20495.

Figs. 5, 5*a*. *Leymeriella* (*Epileymeriella*) cf. *hitzeli* (Jacob). Fragment of adult body-chamber showing *Callizoniceras*-like constrictions and ventral ribbing. Locality and horizon as for Fig. 2. W.W. 15863.

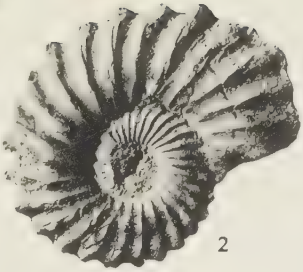
Figs. 6, 6*a*. *Leymeriella* (*Leymeriella*) *diabolus* sp. nov. Side view (6) and restored whorl-section (6*a*) of holotype. Condensed Regularis-Mammillatum beds (Band II), Arnold's Pit, Leighton Buzzard, Beds. W.W. 8084.

Figs. 7, 7*a*. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *densicostata* Spath. Locality and horizon as for Fig. 6. W.W. 16991.

Figs. 8, 8*a*. *Leymeriella* (*Leymeriella*) *consueta* sp. nov. Coarse form leading to var. *magna* nov. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1308.



1



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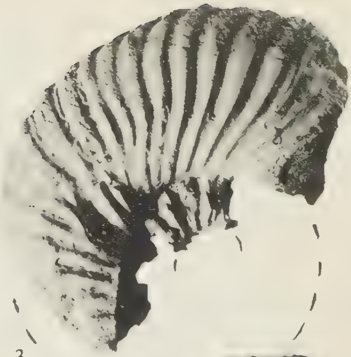

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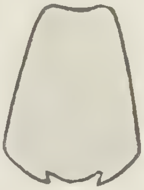
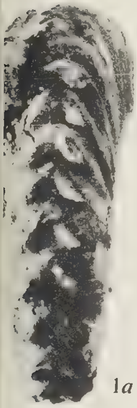
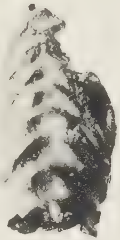


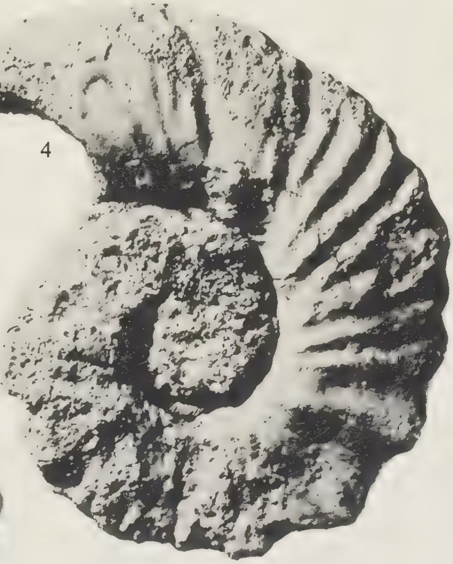
4*a*



1*a*



5*a*



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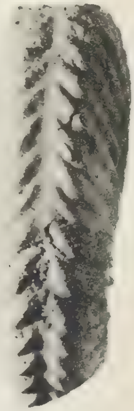
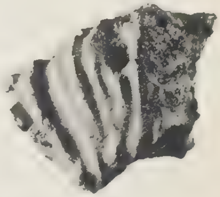


3*a*



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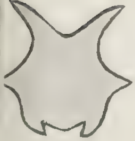
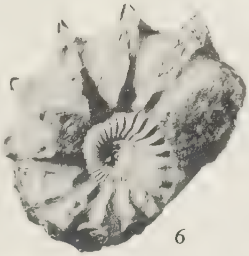


6*a*



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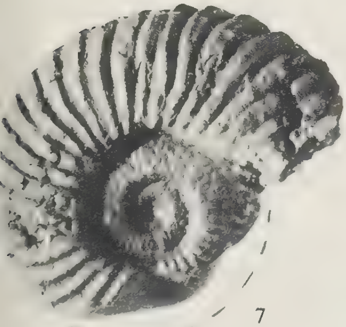

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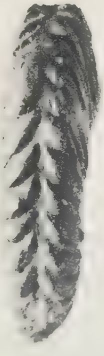
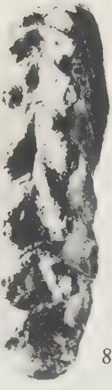
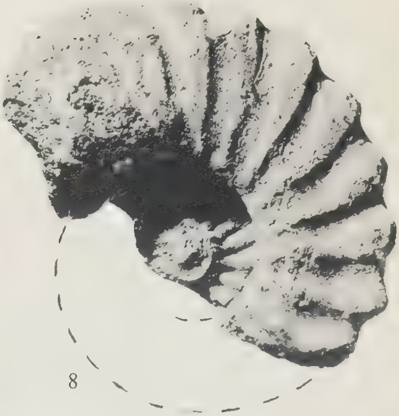


7*a*



8*a*



8

CASEY, *Leymeriella* from Britain

conforms to the familiar pattern of condensed deposition and polyzonal representation so prevalent in the French Albian.

Leymeriella regularis, *L. pseudoregularis*, and *L. tardefurcata* are all associated in the same rock in the derived 'Gault' boulders of Jutland (Skeat and Madsen 1898, pl. 8, pp. 71–74), just as they occur together in England.

Using the threefold subdivision of the Tardefurcata Zone employed by Spath, the following table shows the stratigraphical occurrences of the various genera and species of Leymeriellinae:

	Schrammeni Subzone	*Acuticostata Subzone*	*Regularis Subzone*	*Mammillatum Zone*
Proleymeriella anterior (Brinkmann)	×			
P. schrammeni (Jacob)	×			
P. lemoinei (Jacob)		?		
P. phoenix sp. nov.	×			
Leymeriella (*L.*) *acuticostata* (Brinkmann)		×		
L. (*L.*) *germanica* nom. nov.		×		
L. (*L.*) *tardefurcata* (Leym. MS., d'Orb.)		?	×	
var. *intermedia* Spath			×	
var. *densicostata* Spath			×	
L. (*L.*) *crassa* Spath			×	
L. (*L.*) *romani* Jacob		?	?	
L. (*L.*) *rencurelensis* Jacob		?	×	
L. (*L.*) *revili* Jacob		?	?	
L. (*L.*) *sp. nov.* aff. *revili* Jacob			×	
L. (*L.*) *renascens* Seitz			×	
L. (*L.*) *pseudoregularis* Seitz			×	
L. (*L.*) *heimi* Seitz			?	
L. (*L.*) *fussenegeri* Seitz			?	
L. (*L.*) *andrussovi* Natsky			×	
L. (*L.*) *consueta* sp. nov.			×	
var. *magna* nov.			×	
L. (*L.*) *jacobi* Spath			?	
L. (*L.*) *rudis* sp. nov.			×	
L. (*L.*) *diabolus* sp. nov.			×	
L. (*Epileymeriella*) *hitzeli* Jacob			×	
Pseudoleymeriella haidaquensis (Whiteaves)			?	?

ECOLOGY OF LEYMERIELLINAE

Leymeriella is found in a great variety of neritic deposits, ranging from smooth, soapy clays to coarse sandstones. In Britain and France the principal source of the genus is in the marginal areas of transgression, characterized by shallow-water sediments that carry evidence of inhibited deposition in the presence of glauconite, remanié fossils and rolled phosphatic nodules. At Shenley Hill, Leighton Buzzard, Bedfordshire, where the phosphorite-facies of the Tardefurcata Zone is replaced within a few hundred yards by a brachiopod-rich limestone, the occurrence of *Leymeriella* is exceptional, though it is by no means uncommon in the phosphorites of neighbouring exposures.

There is evidence that the distribution of *Leymeriella* was controlled by ecological factors that acted differentially upon the ammonite faunas. In north Germany, where the development of *Leymeriella* is most complete, the associated ammonite fauna is poor, consisting of species of *Hypacanthoplites* (survivors from the Aptian) and rare *Cleoniceras*; there are no Hoplitinae. On the other hand, during the deposition of the lower two-thirds of the Tardefurcata Zone Leymeriellinae seem to have been completely excluded from the British area, though free communication with north Germany had been established since Valanginian times. The only known ammonite-bearing deposit of early Tardefurcata age in Europe besides that of north Germany is contained in the Folkestone Beds of the Farnham area of Surrey. Here is preserved a rich fauna dominated by the Hoplitid ammonite *Farnhamia*, together with species of *Hypacanthoplites* and *Anadesmoceras* (Casey 1954, p. 108); there are no Leymeriellinae. Stratigraphical investigations in the Lower Greensand have shown that the supposed association of *Leymeriella* with *Sonneratia* and other Hoplitid genera at the junction of the Tardefurcata and Mammillatum Zones is due to collection from condensed deposits. Wherever the two zones are separated, *Leymeriella* and Hoplitids are never found in association. At Wrecclesham, Surrey, for example, the faunal associates of *Leymeriella* consist of the Cleoniceratids *Anadesmoceras* and *Cleoniceras*, and rare *Hypacanthoplites* and *Pictetia*, and it is only in the overlying nodule-beds of the Mammillatum Zone that Hoplitinae such as *Sonneratia*, *Protohoplites*, *Hemisonneratia*, *and Otohoplites* appear. There is in fact no authenticated record of the occurrence of *Leymeriella* or *Proleymeriella* with a member of the Hoplitinae; for even Skeat and Madsen's '*Hoplites splendens* var. *fittoni*', found with *Leymeriella* in the Jutland Drift is not an *Anahoplites* as supposed by Spath (1943, p. 729) but a species of *Anadesmoceras*. The abrupt exit of *Leymeriella* at the height of its prosperity is no less remarkable than the sudden entry of new, virile Hoplitid stocks in Europe, in the Mammillatum Zone. And since these Hoplitid genera are merely specialized developments from *Farnhamia* of the basal Tardefurcata Zone, it is difficult to avoid the conclusion that the Leymeriellinae and the Hoplitinae were mutually exclusive, the one shunning areas favourable to the other.

SYSTEMATIC ACCOUNT OF BRITISH OCCURRENCES OF *LEYMERIELLA*

In Britain only the Regularis Subzone, the topmost part of the Tardefurcata Zone, yields *Leymeriella*. The principal fossiliferous exposures of this subzone are at Leighton Buzzard, Bedfordshire, and at the village of Wrecclesham, near Farnham, Surrey. The succession at the former locality, described by Lamplugh and Walker (1903), Kitchin and Pringle (1920), and Lamplugh (1922), has been revised in detail by Wright and Wright (1947). The *Leymeriella*-bearing horizons occur at the junction of the Gault and Lower Greensand (Folkestone Beds) and consist of two bands of phosphorite nodules; the lower, Band I, contains Regularis fossils only; the higher, Band II, is a remanié deposit of Regularis and early Mammilatum age. Chamberlain Barn and Arnold's Pits are the chief collecting grounds. The Shenley Limestone of Shenley Hill, Leighton Buzzard, is the approximate lateral equivalent of Band I but yields *Leymeriella* only very rarely. The Wrecclesham occurrence has been described by the author (Casey 1951). Here the Regularis Subzone is preserved at the top of the Folkestone Beds as a thin band of phosphorite nodules (Bed 5) with an underlying zone of incipient phosphatization (Beds 2–4). At the type locality of the Folkestone Beds, at East Cliff, Folkestone, Kent, the Regularis Subzone is represented by about 50 feet of yellowish, coarse sands with bands of glauconitic and calcareous sandstone that yield *Leymeriella* sparingly (Casey 1950). In east Sussex there are poor exposures of a nodule-bed with a remanié fauna of

Regularis-Mammilatum age at the base of the Gault in the neighbourhood of Chalvington and Berwick. Isolated finds of *Leymeriella* have been reported from these exposures (Casey 1950). The slipped section of the Speeton Clay of Speeton, Yorkshire, occasionally affords glimpses of a thin nodular greensand seam (Bed A 4) with rare *Leymeriella* (*Epileymeriella*) cf. *hitzeli* (Jacob). Fossils are very irregularly distributed in these phosphorite beds. I have recorded an instance where several hours' search in the Regularis Subzone of Wrecclesham was rewarded by the discovery of but a single fossiliferous nodule, about three cubic inches in volume, but which contained no less than fourteen small specimens of *Leymeriella* (Casey 1951, p. 98). Such 'graveyard' nodules are familiar to every collector from this horizon. Evidently the beds containing them are the remanié *in situ* of several seams of phosphorite nodules, most of which were unproductive of fossils.

In the following account the symbols G.S.M., B.M., and W.W. are used to discriminate the registration numbers of specimens in the collection of the Geological Survey Museum, the British Museum (Natural History), and the Wright brothers. Measurements of ammonites are given in the following order: diameter in mm., height of the outer whorl, thickness of the same, width of the umbilicus, the last three being in percentages of the diameter. Where two diameters are given, the figure in brackets indicates the size at which the percentages were determined.

For the purposes of zoological nomenclature the term 'variety' as used herein has the status of a subspecies.

Leymeriella (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp.

Plate 7, fig. 9; Plate 8, figs. 1–3, 8, 8*a*; Plate 9, fig. 1; Plate 10, figs. 10–11

Ammonites tardefurcatus Leymerie, d'Orbigny 1841, p. 248, pl. 71, figs. 4–5.
Ammonites tardefurcatus Leymerie 1842, p. 16, pl. 18, figs. 3*a*, *b*.
Ammonites tardefurcatus Leymerie, Pictet 1847 (*in* Pictet and Roux), p. 76, pl. 7, figs. 4*a*, *b*.
Ammonites canteriatus nudus Quenstedt 1847, p. 152.
non *Hoplites tardefurcatus* Leymerie sp., Wollemann 1904, p. 37, pl. 5, fig. 6.
Hoplites (*Leymeriella*) *tardefurcatus* Leym. sp., Jacob 1908, p. 52, pl. 7, figs. 9–12.
? *Leymeriella tardefurcata* Leym., Sinzow 1913, pl. 4, figs. 37, 37*a*; (*non* figs. 38, 38*a*, 39).
Leymeriella tardefurcata (Leymerie) d'Orbigny sp., Spath 1925, pp. 84–86, pl. 7, fig. 1; pl. 8, fig. 3; text-fig. 17; (*non* pl. 6, fig. 12).
Leymeriella tardefurcata Leym., Roman 1938, p. 361, fig. 36, 341.
Leymeriella tardefurcata (Leym.) d'Orb., Basse 1952, pl. 20, figs. 4, 4*a*.
non *Leymeriella tardefurcata* Leym., Eristavi 1955, p. 135, pl. 6, fig. 11.

Type. Leymerie's example from the Aube, figured by d'Orbigny (1841, pl. 71, figs. 4–5) has been generally quoted as the type of this species (Spath 1925, p. 84; Brinkmann 1937, p. 12; Roman 1938, expl. fig. 36, 341), though there is no record of re-examination of the actual specimen or specimens. D'Orbigny's figures are so often synthetographs that it is doubtful if the citation of one of his illustrations without reference to the original constitutes a valid lectotype designation. My attempts to trace the Leymerie Collection have so far been unsuccessful. The only specimens specifically mentioned by d'Orbigny in his account of the species that I have been able to locate are Raulin's specimens from Varennes (Meuse), now in the École des Mines, Paris. The best of these is here illustrated in Pl. 8, figs. 2, 2*a*, and it may be necessary to select this specimen as neotype if the Leymerie Collection proves to be no longer extant.

Description of typical form. The ammonite is discoidal, compressed, with subrectangular whorl-section and shallow umbilicus. The whorl reaches its greatest thickness just above the umbilicus and from here the flattened sides narrow slightly to a subtabulate venter that bears a rounded median concavity. For the greater part of life the umbilicus measures about one-third the diameter, but dilates at maturity; the umbilical wall, at first low, fairly steep, and rounded, later becomes flat and oblique. Costation is close, about 35 ribs at 30 mm. diameter, 40 at 50 mm. diameter. The ribs commence at the umbilical suture and are inclined forwards on the flank. They are thin and sharp on the lower part of the flank, but from a point just below mid-flank they expand into narrow, flattened, sulcate wedges. The course of the ribs across the flank varies from almost straight, through slightly curved to gently sigmoidal. Ventrally the ribs terminate in slight clavi that are directed slant-wise forwards across the venter, but fail to connect, leaving a smooth siphonal band. At very large diameters there may be a return to a *Proleymeriella* type of ornament, with shallow constrictions, no tubercles, and the ribs united in chevrons across the venter. A broad, bifid external saddle and small, nearly symmetrical, trifid first lateral lobe characterize the suture-line.

Measurements

W.W. 13603	*c.* 60 (50),	·40,	·33,	·38	Leighton Buzzard. One-third whorl body-chamber.
,,	(30),	·40,	?,	·33	
Jacob, pl. 8, fig. 12	35,	·40,	·29,	·29	Près de Rencurel (Isère).
Raulin Coll. (École des Mines)	30,	·40,	·30,	·33	Varennes (Meuse). Septate.
G.S.M. 31606	21,	·40,	·30,	·30	Leighton Buzzard. Septate.

Remarks. Although d'Orbigny credited the combination *Ammonites tardefurcatus* to Leymerie, his own description and illustration of the species in 1841 first gave validity to the name and established d'Orbigny as its author for the purposes of zoological nomenclature. Nevertheless, most authors who have discussed this nominal species attribute it to Leymerie, whose account appeared in 1842 (Leymerie 1842, p. 16, pl. 18, figs. 3*a*–*b*).

The many records of *L. tardefurcata* from England, France, Switzerland, Germany, and Transcaspia, not to mention reports of the species from the Carpathians, the Urals, and Greenland, would lead one to suppose that this ammonite is well documented and fully described. On the contrary, despite its frequent citation in the literature and its use in stratigraphy, it cannot be considered adequately known. It has been rarely figured photographically, and then only by immature specimens. Jacob's Isère example of 35 mm. (Jacob 1908, pl. 7, figs. 12*a*–*c*) is not fully grown as he supposed, for specimens of twice that size are found in the Lower Greensand. In the absence of adult topotype material for comparison, however, the identification of the larger Lower Greensand specimens is perhaps not above criticism. A Leighton Buzzard example of 60 mm. diameter (Pl. 10, fig. 11) shows a sudden change to a much coarser style of ribbing on the body-chamber, and in an even larger specimen from Wrecclesham (Pl. 9, figs. 1, 1*a*) this coarse stage is followed again by closer ribbing, now uniting in chevrons on the venter in the manner of *Proleymeriella*. If the characters of these two specimens typify those of the normal adult *L. tardefurcata* the 'varieties' *intermedia* and *densicostata*, discussed below, are probably too distinct to be united with this species.

Apart from the named varieties just mentioned, *L. tardefurcata* s.s. itself shows a certain amount of mutability. This occurs principally in two features, the flexuosity of the ribbing and the diameter at which the umbilical wall takes on a gentle gradient. There are also passage forms to the var. *intermedia* and var. *densicostata*, both distinguished by more open umbilici and, in the one case, more distant, and in the other, closer ribbing on the inner whorls.

Strictly interpreted, *L. tardefurcata* is a fossil of the Regularis Subzone and records of the species from earlier strata require confirmation. The use of *L. tardefurcata* as a zonal or subzonal index fossil for beds below the level of *L. regularis* in Germany (Stolley 1908; Brinkmann 1937) and France (Breistroffer 1947) is open to challenge. Collections of *Leymeriella* from the middle of the Tardefurcata Zone of north Germany examined by me in the Paris museums and in the possession of the Wright brothers do not contain a single specimen of the true *L. tardefurcata*, although there are a number of *tardefurcata*-like forms, including *L. germanica* nom. nov. (= *L. tardefurcata anterior* Brinkmann (1937, p. 9, fig. 9). The subspecific name *anterior* was already employed by Brinkmann in the combination *Leymeriella schrammeni anterior* and cannot be used again in the same genus.) Owing to the prevalence of condensed deposition in the *Leymeriella*-bearing beds of France, records of the present species from that country give inconclusive evidence of horizon.

Leymeriella (*Leymeriella*) *tardefurcata* var. *densicostata* Spath

Plate 9, figs. 7, 7*a*; Plate 10, figs. 9, 9*a*, 12

Hoplites (*Leymeriella*) *tardefurcatus* Leym. sp., variété à côtes serrées, Jacob 1908, pl. 7, figs. 13*a*, *b*.
Leymeriella tardefurcata (Leymerie) d'Orbigny sp. var. *densicostata* Spath 1925, p. 85, pl. 7, fig. 2.
Leymeriella tardefurcata Leym. in d'Orb. sp. var. *densicostata* Spath, Breistroffer 1931, p. 194.
Leymeriella tardefurcata Leym. sp. var. *densicostata* Spath, Breistroffer 1947, p. 23.

Type. The example figured by Spath (1925, pl. 7, fig. 2) from the condensed Tardefurcata-Mammillatum Zones of Chamberlain Barn Pit, Leighton Buzzard, Beds. (L. F. Spath Coll. no. 977).

Description. This variety is distinguished by the relatively rapid widening of its umbilicus and by its densely ribbed inner whorls, possessing 50–55 ribs at 30 mm. diameter as compared with an average of 35 in the typical form.

Measurements

W.W. 16991	47, ·40, ·28, ·40	Leighton Buzzard. Half-whorl body-chamber.
W.W. 19703	27, ·42, ·30, ·30	Leighton Buzzard (Band II).

Remarks. Specimens of this variety hitherto figured and described are immature. It is now possible to see from material more representative of the different stages of growth that the dense ribbing which makes this variety so easily separable at 30 mm. diameter does not persist into the adult, which at 40–50 mm. diameter has costation precisely the same as that of the typical *L. tardefurcata*. A Wrecclesham example (G.S.M. Zm 1286), previously recorded (Casey 1951, p. 97) as *L.* aff. *tardefurcata*, has dimensions 53, ·39,

·30, ·34, and is intermediate between this var. *densicostata* and *L. tardefurcata* s.s. Specialization in dense ribbing is carried to a more advanced stage in *L. revili* Jacob (1908, pl. 7, figs. 16*a*, *b*).

Leymeriella (*Leymeriella*) *tardefurcata* var. *intermedia* Spath

Plate 10, figs. 2, 6, 8, 8*a*

? *Ammonites canteriatus* Brongniart, Quenstedt 1849, pl. 10, figs. 13*a*, *b*.
? *Leymeriella tardefurcata* Leym., Sinzow 1913, pl. 4, fig. 39 only.
Leymeriella tardefurcata (Leymerie) d'Orbigny sp. var. *intermedia* Spath 1925, p. 85 (pars) pl. 6, fig. 12.
Leymeriella tardefurcata intermedia Spath, Wright and Wright 1947, p. 166 (pars).
Leymeriella intermedia Spath, Casey 1951, p. 97 (pars).

Type. The example figured by Spath (1925, pl. 6, fig. 12) from the condensed Tardefurcata-Mammillatum Zones of Billington Crossing, Leighton Buzzard, Beds. (G. W. Lamplugh Coll.).

Description. This variety is characterized by the relatively rapid widening of the umbilicus and by having inner whorls that are slightly more coarsely ribbed, bear more distinct peripheral clavi, and give a hint of tuberculation just above the umbilicus.

EXPLANATION OF PLATE 10

Fig. 1. *Leymeriella* (*Leymeriella*) *pseudoregularis* Seitz. Adult example. Regularis Subzone (Bed 5), Wrecclesham, Surrey. G.S.M. Zm 1289; author's Coll.

Fig. 2. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *intermedia* Spath. Dwarf form. Regularis Subzone (Band I), Arnold's Pit, Leighton Buzzard, Beds. W.W. 18038.

Figs. 3, 3*a*. *Leymeriella* (*Leymeriella*) *consueta* var. *magna* nov. Adolescent body-chamber. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1295.

Fig. 4. *Leymeriella* (*Leymeriella*) *renascens* Seitz. Condensed Regularis-Mammillatum beds (exact bed unknown), Arnold's Pit, Leighton Buzzard, Beds. W.W. 16106.

Figs. 5, 5*a*–*b*. *Leymeriella* (*Leymeriella*) *consueta* sp. nov. Side view (5), ventral view (5*b*), and whorl-section (5*c*) of nucleus. Regularis Subzone (Band I), Arnold's Pit, Leighton Buzzard, Beds. W.W. 9741.

Fig. 6. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *intermedia* Spath. Adult example. Locality and horizon as for Fig. 5. W.W. 17949.

Fig. 7. *Leymeriella* (*Leymeriella*) *regularis* (Bruguière) d'Orbigny sp. Body-chamber fragment. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1306.

Figs. 8, 8*a*. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *intermedia* Spath. Coarsely ribbed form leading to *L.* (*L.*) *regularis*. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1288.

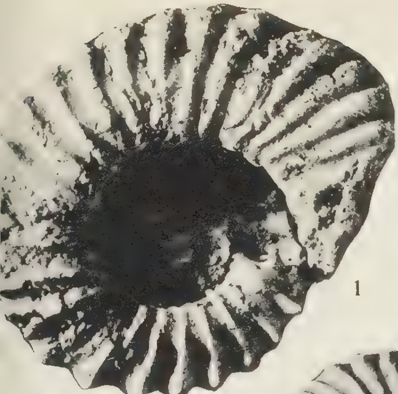
Figs. 9, 9*a*. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *densicostata* Spath. Side view (9) and whorl-section (9*a*) of example with coarsely ribbed inner whorls, transitional from *L.* (*L.*) *tardefurcata* s.s. Regularis Subzone (Bed 4), Wrecclesham, Surrey. G.S.M. Zm 1286; author's Coll.

Fig. 10. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp. Immature example. Locality and horizon as for Fig. 4. G.S.M. 31606.

Fig. 11. *Leymeriella* (*Leymeriella*) *tardefurcata* (Leymerie MS.) d'Orbigny sp. *s.l.* Large example showing coarsely ribbed body-chamber. Locality and horizon as for Fig. 4. W.W. 13603.

Fig. 12. *Leymeriella* (*Leymeriella*) *tardefurcata* var. *densicostata* Spath. Immature example. Condensed Regularis-Mammillatum Beds (Band II), Arnold's Pit, Leighton Buzzard, Beds. W.W. 19703.

Fig. 13. *Leymeriella* (*Leymeriella*) *consueta* sp. nov. Holotype. Locality, horizon, and collector as for Fig. 1. G.S.M. Zm 1307.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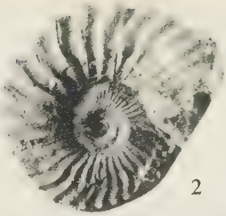
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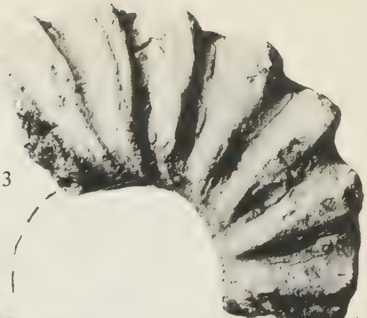
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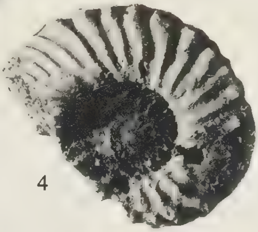
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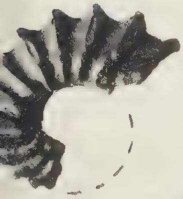

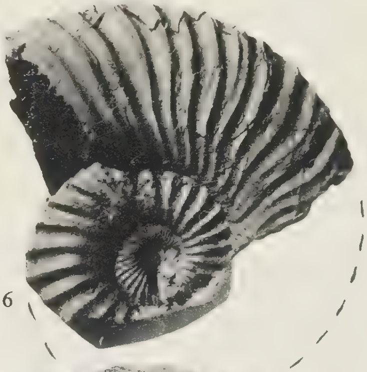
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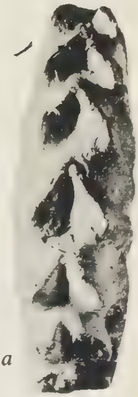
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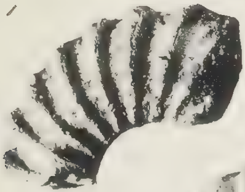
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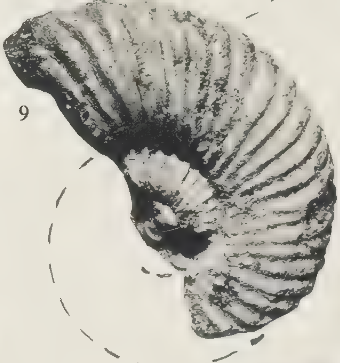
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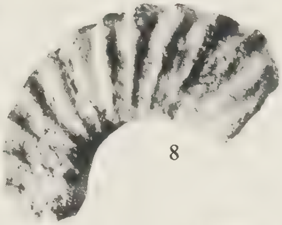
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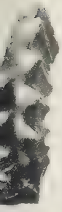
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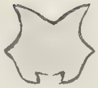
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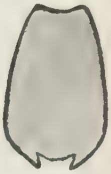
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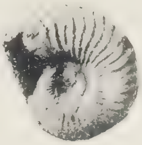
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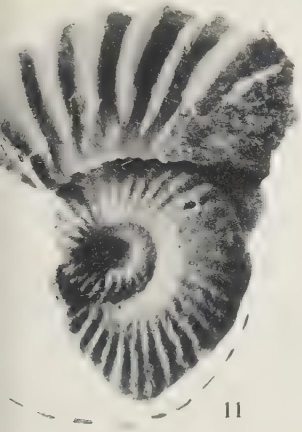
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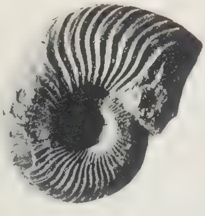
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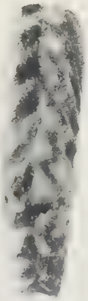
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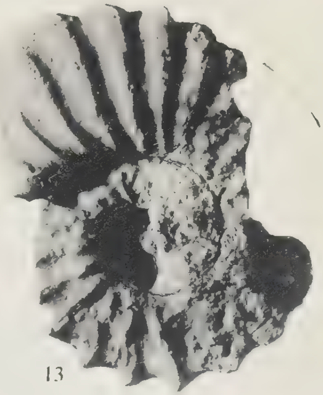
13

CASEY, *Leymeriella* from Britain

Measurements

W.W. 17949	*c.* 55 (46), ·38, ·30, ·39	Leighton Buzzard (Band I). Half-whorl body-chamber.
D'Orbigny Coll.	47, ·38, ·29, ·40	Machéroménil. Half-whorl body-chamber.
W.W. 16038	27, ·38, ·27, ·39	Leighton Buzzard. Half-whorl body-chamber.

Remarks. This variety links *L. tardefurcata* with *L. regularis*, though morphologically it is closer to the former of the two. In the case of immature or fragmentary material identification of this variety should not lightly be attempted, for it is not distinguished from *L. consueta* until 20 mm. diameter, while the coarsely ribbed stage which is its chief point of difference from *L. tardefurcata* s.s. is transitory, and although of variable duration is always confined to the young. Normally, by 30 mm. diameter the costation is no different from that of the typical *L. tardefurcata*, though in transitions to *L. regularis* it may remain distinct until 45 mm. diameter. On the other hand, variation in the opposite direction leads to a form like that from Machéroménil illustrated in Pl. 8, fig. 1. This is separable from *L. tardefurcata* s.s. only by the wider umbilicus and the slightly emphasized ventral clavi of the young.

The small example listed in the table of measurements and illustrated in Pl. 10, fig. 2 is a dwarf. The open umbilicus and closing up of the ribs towards the end indicate that it is fully grown at 27 mm. diameter.

Leymeriella fussenegeri Seitz, from Vorarlberg (Rhaetic Alps), seems to be one of these transitions from *L. tardefurcata* var. *intermedia* to *L. regularis*, differing from the typical form of *intermedia* only in its more definite suggestion of bituberculation on the inner whorls. It is doubtful if it merits a separate name.

Leymeriella rencurelensis Jacob is allied to this variety, but has uniformly coarse ribbing and stouter whorls. Jacob's fragment of '*Hoplites* (*Parahoplites*) sp.' from Isère (Jacob 1908, pl. 7, figs. 5*a*–*b*), renamed *Leymeriella jacobi* by Spath (1925, p. 75), seems to be distinguishable from the present form at 45 mm. diameter only by a small increase in the thickness of the whorl.

Distribution. (Typical form and var. *intermedia*) ubiquitous in the Regularis Subzone of south-east England. (Var. *densicostata*) Band II, Arnold's Pit, Billington Crossing, Leighton Buzzard, Bedfordshire, and Bed 4, Wrecclesham, Surrey.

Leymeriella (*Leymeriella*) *regularis* (Bruguière) d'Orbigny sp.

Plate 8, figs. 5, 5*a*, *b*, 9, 9*a*; Plate 9, fig. 2; Plate 10, fig. 7

? *Ammonis cornu* Langius 1708, p. 95, pl. 24, fig. 2.
? *Ammonites regularis* Bruguière 1789, p. 42, no. 19.
? *Ammonites canteriatus* (Defrance), Brongniart (*in* Cuvier and Brongniart) 1882, pl. 6, fig. 7.
Ammonites regularis Bruguière, d'Orbigny 1841, p. 245, pl. 71, figs. 1, 2 (not fig. 3).
Ammonites canteriatus nodosus Quenstedt 1847, p. 152.
Hoplites regularis Brug., Skeat and Madson 1898, p. 198 (pars), pl. 8, figs. 6, 8 (only).
non *Hoplites* (*Leymeriella*) *regularis* Brug. sp., Jacob 1908, pl. 17, figs. 23–24.
Leymeriella regularis (Bruguière) d'Orbigny sp., Spath 1925, p. 86, pl. 6, figs. 13*a*, *b*; pl. 8, fig. 4; text-fig. 18 (*non* pl. 7, fig. 3).
non *Leymeriella regularis* (Brug.) d'Orb., Seitz 1930, p. 21, pl. 4, figs. 2*a*, *b*; text-fig. 3*a*.
Leymeriella aff. *regularis* Bruguière, d'Orbigny sp., Casey 1950, p. 292, pl. 14, figs. 11*a*, *b*.

Neotype (here selected). A specimen in the Raulin Collection in the École des Mines, Paris (Pl. 8, figs. 5, 5*a–b*) from the condensed Tardefurcata-Mammillatum Zones of Sauces, near Novion (Ardennes), apparently used for d'Orbigny's pl. 71, figs. 1–2.

Description. To a diameter of 12–15 mm. this species resembles *L. tardefurcata.* Thereafter the ribbing becomes increasingly distantly spaced, and the appearance of umbilical flares and ventral clavi cause the whorl-section to change from subrectangular to hexagonal. When the ornament is fully developed, at 25–30 mm. diameter, the whorls bulge at the umbilical flares, are slightly concave at the sides, and have the venter excavated in the form of a V. The ribs commence just above the umbilical suture and lean forwards as they cross the gentle umbilical slope to merge into the umbilical flare; here they are thin and sharp. On leaving the umbilical flare they strike across the flank in a line that is almost straight or gently concave forwards; here they are flat, ribbon-like, broaden towards the venter and bear a shallow median depression. At the ventro-lateral margins they are elevated into prominent triangular clavi that lean outwards from the flank and are prolonged faintly obliquely forwards on the venter, each pair of clavi thus producing a faint chevron with the apex cut off by the bottom of the ventral sulcus. At 35 mm. diameter the ribs number 20–25. The umbilicus is at first about one-third of the diameter, but widens a little during growth. Decline in strength of the sculpture takes place at varying diameters after 25 mm. The umbilical flares lose height and move closer to the margin of the umbilicus, the umbilical slope becomes steeper, the ventral clavi less projecting, and the costation more closely spaced.

Measurements

B.M. C 40348	*c.* 40 (36), ·40, ·33, ·36	Leighton Buzzard.	Half-whorl body-chamber
Neotype	35, ·40, ?, ·35	Sauces (Ardennes).	„ „
W.W. 18812	30, ·40, ·33, ·34	Leighton Buzzard.	„ „
G.S.M. 31607	27, ·39, ·33, ·33	„ „	„ „
B.M. L.F.S. 986	21, ·40, ·32, ·32	„ „	„ „

Remarks. Leymeriella regularis is involved in difficulties all too familiar to the palaeontologist dealing with old-established specific names. Its use in stratigraphy as an index fossil is threatened both by doubts as to the identity of the species which should rightfully bear the name and by conflicting opinions as to the horizon of the species which customarily passes for *L. regularis.*

Bruguière did not himself illustrate the species when proposing the name *Ammonites regularis*, but referred to a specimen figured in an early-eighteenth-century work (Langius 1708, pl. 24, fig. 3). This specimen is no longer extant and the illustration is quite inadequate for recognition of the species by present-day standards. The modern interpretation of *A. regularis* dates from its illustration by d'Orbigny (1841, pl. 71, figs. 1–3) and it is d'Orbigny's original, from the Albian of the Ardennes, which for over a century has assumed the role of type specimen. Although the great majority of workers have been content to accept d'Orbigny's authority concerning the identity of *A. regularis*, Quenstedt was a dissentient. He supposed Langius's original to be a Liassic *Schlotheimia* and regarded d'Orbigny's specimen as a variety of *A. canteriatus* Defrance, styling it

A. canteriatus nodosus. Owing to the prior use of the name *Ammonites nodosus* by de Roissy (1805), Schlotheim (1813), and J. Sowerby (1815), we are not obliged to revive Quenstedt's name for this species.

I am of the opinion that in view of its use in stratigraphy and long standing in the literature, the name *A. regularis* should be retained with the meaning given it by the majority of workers. Application will therefore be made to the International Commission on Zoological Nomenclature for the recognition of a neotype selection for *A. regularis* that will realize this objective. The original (or one of the originals) of d'Orbigny's pl. 71, figs. 1–2 is the ideal choice for neotype.

D'Orbigny (1841, p. 248) stated that his figured specimen had been collected by J. Raulin from Sauces, in the Machéroménil neighbourhood of the Department of Ardennes, that it retained the test, and that it was reproduced natural size. The École des Mines, Paris, possesses a specimen of *L. regularis* in the Raulin Collection from that locality. It has the test preserved and was almost certainly used in d'Orbigny's illustration. The specimen is partly enclosed in a phosphorite nodule and ends at a natural break at about 35 mm. diameter. This break runs obliquely forwards and downwards and corresponds to the crack illustrated in d'Orbigny's drawing at 42 mm. diameter. In my opinion d'Orbigny's illustration is a synthetograph, composed of a slightly enlarged reproduction of Raulin's specimen with the last half-whorl added from another specimen or from imagination. I have seen no examples of *L. regularis* as large as d'Orbigny's holograph, and it is possible that this last half-whorl was restored from a specimen of *L. consueta*, specimens of which are labelled *A. regularis* in the d'Orbigny Collection. I believe that the suture-line (d'Orbigny 1841, pl. 71, fig. 3) attributed to *A. regularis* was drawn from the holotype of *L. rudis* sp. nov., another of d'Orbigny's Machéroménil '*A. regularis*'. It is proposed to designate the specimen in the Raulin Collection (Pl. 8, figs. 5, 5*a*, *b*) neotype of *A. regularis* Bruguière.

A form of *Leymeriella* differing from *L. regularis* in its greatly increased whorl-thickness was separated by Spath (1925, p. 87) under the name *L. regularis* var. *crassa*. To this variety were referred Jacob's *forme épaisse* of *L. regularis* and a single specimen from Leighton Buzzard. The latter is an execrable fragment, hardly more than 22 mm. in diameter, and was illustrated by Spath only in a sectional outline, enlarged and greatly restored (Spath 1925, pl. 7, fig. 3). Up to 20 mm. diameter the specimen exhibits characters normal to a compressed *Leymeriella* of the *regularis-consueta* type; on the final portion of the ammonite the whorl suddenly expands and at the same time the sides develop crippled ribs. It is an obvious malformation. Despite the fact that this specimen is labelled 'holotype' in the British Museum collections, we are not bound to accept it as such, since no type selection was made either in the original or in subsequent publications. Jacob's *L. regularis*, *forme épaisse*, from Goudinière (Haute-Savoie) (Jacob 1908, pl. 7, figs. 24*a*, *b*), one of the syntypes of this 'variety', is here designated lectotype of *L. crassa* Spath. In according this taxon specific rank I follow Breistroffer (1947, p. 70), for *L. crassa* is not only more inflated than *L. regularis*, but also more strongly tuberculate, its ribs more deeply sulcate. The species has not yet been found in England.

Distribution. Regularis Subzone. Folkestone Beds (Bottom Stone Band), East Cliff and Mill Point, Folkestone; Beds 4 and 5, Wrecclesham, Surrey; Bed 7, Chalvington, Sussex; Bands I and II, Arnold's and Chamberlain Barn Pits, Leighton Buzzard, Bedfordshire.

Leymeriella (*Leymeriella*) *pseudoregularis* Seitz

Plate 10, fig. 1

Hoplites regularis Brug., Skeat and Madson 1898, p. 198 (pars), pl. 8, fig. 4.
Hoplites (*Leymeriella*) *regularis* (Bruguière), Jacob 1908, pl. 7, figs. 23*a*, *b* only.
Leymeriella pseudoregularis Seitz 1930, p. 24, pl. 5, fig. 3.
Leymeriella canteriata Defr. in Brongn. sp., Breistroffer 1947, p. 70.
Leymeriella pseudoregularis Seitz, Casey 1950, pp. 292–3.
Leymeriella canteriata Brong. var. *pseudoregularis* Seitz, Breistroffer 1957 (*in* Rosset), p. 40.

Holotype. The specimen figured by Seitz (1930, pl. 5, fig. 3) from the Lower Albian of Plattenwald (Vorarlberg), Rhaetic Alps.

Description. This species differs from *L. regularis* in being more evolute and in developing flattened or grooved ribs only at an advanced stage of growth. The early whorls are more coarsely ribbed and more inflated than those of *L. regularis* at a similar diameter and tuberculation is rather more pronounced. The few available adult specimens suggest that the untuberculated, closely ribbed stage commences comparatively early. The suture-line agrees with that of *L. consueta*.

Measurements

G.S.M. Zm 1289	60,	·35,	·25,	·43	Wrecclesham. Septate to 44 mm.
„ „	(32),	·34,	·31,	·42	
*Jacob's pl. 7, fig. 23	32,	·35,	·31,	·42	Près de Rencurel (Isère).
†Seitz's P 47	27·5,	·30,	?·27,	·47	Plattenwald (after Seitz).
Seitz's P 53	25·2,	·345,	·345	·425	„ „
	(13·6),	·37,	—,	·37	„ „

* Corrected measurements. † Ribs and tubercles omitted in measurements.

Remarks. Prior to its separation by Seitz *L. pseudoregularis* was included in the broad '*Hoplites regularis*' of authors. An example of the present species was, indeed, taken by Jacob (1908, pl. 7, figs. 23*a*, *b*) to typify *L. regularis*. A very full discussion of *L. pseudoregularis* was given by Seitz. He described his specimens as varying principally in the degree of prominence of the tubercles, and in consequence also in the whorl-section. The specimen chosen as holotype was considered in this respect to represent the norm. Lower Greensand examples show variation on the same lines as the German types, though they are generally more strongly tuberculate than the holotype, which is now known to be an immature shell. A small example from Berwick Common, Sussex (G.S.M. 38053), identified by Spath (1935, p. 429; 1943, p. 740) and Kirkaldy (1935, p. 523) as *L. regularis* is one of these more spinose variants of *L. pseudoregularis*. At a diameter of 20 mm. it is already distinguishable from juvenile *L. consueta* by reason of its wider umbilicus and the absence of costal sulcations. No examples larger than 32 mm. diameter have been figured previously. Pl. 10, fig. 1 illustrates a specimen of 60 mm. diameter from Wrecclesham which is believed to be adult. It shows loss of lateral tuberculation at a diameter of 45 mm., followed by a denser style of costation on the last half-whorl, which is all body-chamber.

Breistroffer (1947, p. 70) has expressed the opinion that Brongniart's *Ammonites canteriatus* is a senior synonym of *L. pseudoregularis* Seitz. The former species is based on a poor illustration in Cuvier and Brongniart's *Environs de Paris* (1822, pl. 6, fig. 7) and cannot be satisfactorily determined. It does not appear to be stout enough or evolute enough for identification with *L. pseudoregularis*; I think it more likely to be a badly drawn *L. regularis*. In a more recent publication Breistroffer (*in* Rosset 1957, p. 40) treats *pseudoregularis* as a variety of *canteriata*.

Distribution. Regularis Subzone. Folkestone Beds (Bottom Stone Band), East Cliff, Folkestone, Kent; Berwick Common, Sussex; Band II, Arnold's Pit, Leighton Buzzard, Bedfordshire; Beds 4 and 5, Wrecclesham, Surrey.

Leymeriella (*Leymeriella*) *consueta* sp. nov.

Plate 9, figs. 8, 8*a*; Plate 10, figs. 5, 5*a*, *b*, 13; text-fig. 1*a–h*

Hoplites (*Leymeriella*) *sp.* between *H.* (*L.*) *tardefurcatus* Leym. and *H.* (*L.*) *regularis* Brug., Jacob 1908, pl. 7, fig. 22 only.

Leymeriella tardefurcata (Leymerie MS.) d'Orbigny sp. var. *intermedia* Spath 1925, p. 85 (pars).

Leymeriella intermedia Spath, Casey 1951, p. 97 (pars).

Holotype. The example figured in Pl. 10, fig. 13 from the Regularis Subzone of Wrecclesham, Surrey (G.S.M. Zm 1307, author's collection).

Description of typical form. Similar to *L. regularis* but larger and with adolescent whorls that are stouter and more prominently tuberculated, the lateral flare of *L. regularis* being replaced by a distinct spine.

Measurements

G.S.M. Zm 1305	57,	·41,	?,	·37	Wrecclesham. Half-whorl body-chamber.
G.S.M. Zm 1304	54,	·40,	?,	·36	„ „ „
G.S.M. Zm 1307	52,	·39,	·39,	·37	„ „ „
„ „	(33),	·40,	·39,	·33	„ „ „
Jacob 1908, pl. 7, fig. 22	50,	·39,	?,	·36	La Goudinierè (Haute-Savoie).
W.W. 9741	28,	·40,	·41,	·32	Arnold's Pit, Leighton Buzzard, Septate.

Remarks. None of the names at present available for species of *Leymeriella* appears to cover this common form from the Regularis Subzone. A typical example of *L. consueta* from La Goudinière (Haute-Savoie) was figured by Jacob (1908, pl. 7, fig. 22) as a passage form between *L. regularis* and *L. tardefurcata*, and this same specimen was included by Spath (1925, p. 85) in his *L. tardefurcata* var. *intermedia*, a taxon recognized to accommodate such passage forms. But the adolescent whorls of *L. consueta* are much more strongly ornamented than those of *L. regularis* or *L. tardefurcata*, and if these three species are regarded as gradations in a single morphological series, the sequence, from less to more ornate, would be *L. tardefurcata*, *L. regularis*, *L. consueta*. This simple series does not adequately express the relationship of the species now under consideration, for *L. pseudoregularis* Seitz occupies a position in the plexus equally close to *L. consueta*, differing mainly in being less spinose in adolescence and in having grooved ribs only at an advanced stage of growth.

The first volutions of *L. consueta* are indistinguishable from those of *L. tardefurcata* var. *intermedia*, but the resemblance ceases as soon as the coarser ribbing and bituberculation appear. This takes place typically at 20 mm. diameter. Maximum strength of tuberculation is reached generally at 30 mm. diameter; the lateral tubercle then shrinks and moves closer to the umbilical border, so that by 40 mm. diameter the ammonite looks like an enlarged version of *L. regularis*. At a diameter of 50 mm. the ribs average 24 to the whorl.

Leymeriella (*Leymeriella*) *consueta* var. *magna* nov.

Plate 8, fig. 7; Plate 9, figs. 4, 4*a*; Plate 10, figs. 3, 3*a*

? *Ammonites regularis* Bruguière, Pictet 1847 (*in* Pictet and Roux), p. 330, pl. 7, figs. 3*a*–*c*.
? *Leymeriella regularis* Brug. var. nov. Breistroffer 1931, p. 211.

Type. W.W. 20495, Regularis Subzone (Bed 5), Wrecclesham, Surrey.

Description. In this variety distantly spaced ribbing and bituberculation appear earlier than in the typical form and persist to 55–66 mm. diameter.

Measurements

Type	82, ·36, ·30, ·40	Wrecclesham. Septate to 50 mm.

Remarks. The type of this variety is one of the largest specimens of *Leymeriella* that has passed through my hands. The uncoiling body-chamber, with part of a simple mouth-border preserved near the umbilicus, occupies a little more than half a whorl and terminates at 82 mm. diameter. Distinctive, robust ornament, recalling in lateral aspect that of *Neokentroceras speciosum* Haas (1942, pl. 8, figs. 14*c*–*d*), persists on to the posterior part of the body-chamber. Close, flexuous, untuberculated ribbing then intervenes suddenly, the regularity of the ribbing being interrupted on the anterior half of the body-chamber by three shallow constrictions.

D'Orbigny's specimens of *A. regularis* from Novion (Ardennes), in the Museum d'Histoire Naturelle, Paris, include small examples of *L. consueta* var. *magna*, one of which is illustrated in Pl. 8, fig. 7.

Pictet's illustration of *A. regularis* from the Perte du Rhône, listed in synonymy, may have been based on a specimen of the present variety, though the lateral tubercle of the inner whorl has an unusually high position on the flank. Breistroffer's description of a variety of *L. regularis* from Près de Rencurel as being as coarsely ornamented as *L. crassa* though more compressed than that species, fits the present form but cannot be identified as such in the absence of illustrations.

Leymeriella (*Leymeriella*) *rudis* sp. nov.

Plate 7, fig. 10; Plate 8, figs. 6, 6*a*, *b*

Ammonites regularis Bruguière, d'Orbigny 1841, pl. 71, fig. 3 only.
Leymeriella sp. nov. Casey 1951, p. 97.

Holotype. An example in the d'Orbigny Collection (Pl. 8, figs. 6, 6*a*) from the condensed Regularis-Mammillatum horizon of Novion, near Machéroménil (Ardennes), now in the Muséum d'Histoire Naturelle, Paris (No. 5794 pars).

Description. This species combines the coarse and persistent ornament of *L. consueta* var. *magna* with a much more inflated whorl-shape and a more rapidly widening umbilicus. The suture-line has rather narrow saddles.

Measurements

Holotype	50,	·40,	·40,	·40	Septate
Topotype (d'Orbigny Coll.)	44,	·40,	·40,	·38	,,

Remarks. The type and topotype listed above are labelled in the d'Orbigny Collection '*A. regularis*' and '*A. michelinianus*' respectively. Resemblance to the latter, a species of *Protohoplites*, is only superficial but serves to direct attention to the convergence towards the Hoplitidae exhibited by this exceptionally strongly sculptured form of *Leymeriella*. In *L. crassa*, the nearest relative to the present form, the ribs are less widely spaced, the lateral tubercle placed nearer the venter, and the ribs more distinctly looped between the tubercles. The suture-line of this species (probably of the holotype itself) was figured by d'Orbigny as that of *A. regularis*.

Distribution. Regularis Subzone. Band I, Arnold's Pit, Leighton Buzzard, Bedfordshire; Bed 5, Wrecclesham, Surrey. Very rare.

Leymeriella (*Leymeriella*) *renascens* Seitz

Plate 10, fig. 4

Leymeriella renascens Seitz 1930, pp. 29–30, pl. 5, figs. 9*a*, *b*.
Leymeriella renascens Seitz, Breistroffer 1947, p. 23.

Holotype. The specimen figured by Seitz (1930, pl. 5, figs. 9*a*, *b*) from Vorarlberg (Rhaetic Alps).

Description. A widely umbilicated species of *Leymeriella* with early whorls resembling those of *L. consueta* s.s., but with bituberculation less vigorous and terminating early in ontogeny (25–30 mm. diameter), the ammonite then assuming simple ribbing. Towards the end of the body-chamber there is a sudden increase in density of ribbing and reduction in prominence of the ventral clavi. Typically this metamorphosis is completed at 40 mm. diameter.

Measurements

Holotype	39 (30·9),	36,	·32,	·39	Half-whorl body-chamber.
W.W. 16106	32,	35,	·31,	·42	Two-fifths-whorl body-chamber.

Remarks. The most striking features of this species are the wide umbilicus and drastic change in ornament while the ammonite is still at a relatively small diameter. There is a single Lower Greensand specimen, from Leighton Buzzard, which conforms to the characters of the holotype and it acquires the crowded ribbing of the adult at much the same diameter. These specimens may, however, be dwarfs. Another Leighton Buzzard example (B.M. C 36627, Pl. 9, figs. 3, 3*a*) is half of a disk of 55 mm. diameter and has close, *tardefurcata*-type ribbing on the body-chamber and inner whorls that agree with those of the present species. This specimen appears to be conspecific with a Machéroménil example in the d'Orbigny Collection, wholly septate and with dimensions 50, ·36, ·30, ·36. These may represent the 'normal' form of the species. A more doubtful Wrecclesham example (G.S.M. Zm 1296) has a period of crowded ribbing followed, at 45 mm. diameter, by recrudescence of coarse costation, while the umbilicus is only 36 per cent. of the diameter. *Leymeriella heimi* Seitz, so far as it can be assessed by the single distorted specimen figured by Jacob (1908, pl. 7, fig. 21), differs from the present form in its smaller umbilicus and more strongly tuberculated inner whorls.

Distribution. Condensed Tardefurcata-Mammillatum Zones, Arnold's Pit, Billington Crossing, Leighton Buzzard, Beds.; ? Regularis Subzone (Bed 5), Wrecclesham, Surrey.

Leymeriella (*Leymeriella*) *diabolus* sp. nov.

Plate 9, figs. 6, 6*a*

Holotype. An example from the condensed Tardefurcata-Mammillatum Zones (Band II) of Arnold's Pit, Billington Crossing, Leighton Buzzard, Bedfordshire (W.W. 8408).

Description. The whorls are slightly compressed, the intercostal section being rounded-quadrate; a cross-section through the ribs and tubercles of the adult shell approximates to a hexagon with concave sides, the greatest thickness occurring at the lateral tubercle, at mid-flank, the venter being broadly and deeply excavated in the form of a V. The umbilicus measures a little less than one-third the diameter.

Up to a diameter of 10 mm. the costation consists of thin, sharp, closely-spaced ribs that issue from the umbilical suture and lean forwards as they pass over the flanks. Subsequently the ribs become more distantly spaced and are pinched up into flares at the umbilical margin and into triangular clavi at the ventral edges. The outer portion of each rib is split so as to form a loop between the flare and the clavus. At this stage the ammonite resembles *L. regularis.*

The final ornament is assumed between 15 and 20 mm. diameter. This consists of straight, widely-spaced ribs, thin and sharp below, split into triple riblets above; the lateral flares are transformed into a stout spines, positioned at mid-flank, while the ventral clavi become increasingly tall, triangular, flattened horns that bend outwards and slightly backwards. Ridge-like extensions of the clavi run obliquely forwards across the venter, producing very faint chevrons pointing in the direction of growth. Behind the apex of each chevron there is a shallow, oval pit. At 35 mm. diameter the ribs number sixteen, the last half-whorl possessing only six. The suture-line is unknown.

Measurements

Holotype	35, ·43, ?, ·31

Remarks. There is but a single specimen of this species, but it differs so markedly from any form of *Leymeriella* hitherto described that its taxonomic separation is justified. Its special features are the unusually straight ribs, exaggerated tuberculation, and the splitting of the costae into *triple* riblets. No other species of *Leymeriella* possesses costae of this sort, for the double forking of the ribs sometimes seen in *Leymeriella* (*Epileymeriella*) of the *hitzeli* group is quite different. *Leymeriella crassa* Spath is probably its closest relative, having a similar stout whorl and the lateral tubercle placed high up on the whorl-side, though it is considerably less spinose and less distantly ribbed.

The holotype of *L. diabolus* is a complete specimen in the normal phosphatic preservation of the Leighton Buzzard nodule-beds. The last half-whorl is probably body-chamber, though the presence of much of the test makes it difficult to detect the last septal suture. Unfortunately most of the tubercles have suffered damage in the extraction of the ammonite from the matrix.

Distribution. As for holotype.

Leymeriella (*Leymeriella*) sp. nov. cf. *revili* Jacob

Cf. *Hoplites* (*Leymeriella*) *Revili* Jacob 1908, p. 53, pl. 7, figs. 14, 15, 16*a–b*.

Remarks. Two specimens from Leighton Buzzard in the Geological Survey Museum (31837, 31839) represent an undescribed form of *Leymeriella* allied to *L. revili* Jacob. Both are small fragments and are unsuitable as material for diagnosis of a new species. The largest is a segment of one-third of an ammonite of 16 mm. diameter. Its flanks are ornamented with fine, hair-like riblets, about twice as numerous as those of *L. revili* at the same diameter. Future discoveries must decide whether these specimens are juvenile or represent a micromorph species.

Distribution. Condensed Tardefurcata-Mammillatum Zones, Billington Crossing, Leighton Buzzard, Beds.

Leymeriella (*Epileymeriella*) sp. cf. *hitzeli* (Jacob)

Plate 9, figs. 5, 5*a*

Cf. *Hoplites* (*Parahoplites*) *Hitzeli* Jacob 1908, p. 48, pl. 8, figs. 1–3

Remarks. The fragment illustrated in Pl. 9, figs. 5, 5*a* is of more than ordinary interest, for not only is it the only Lower Greensand example of *Epileymeriella* on record, it is also the largest specimen of the subgenus yet known. It is a portion of the body-chamber of an ammonite of about 50 mm. diameter and is 31 mm. long, with a height of 20 mm. and a width of about 16 mm. at the anterior end. The flanks bear three pairs of bifurcating ribs between two deep constrictions; on the venter the ribs are joined into a forward arch. An impression of the dorsum reveals costation similar to that of one of Jacob's syntypes of *L.* (*E.*) *hitzeli* (Jacob 1908, pl. 8, figs. 1*a*, *b*). In view of the proved descent of *Leymeriella* from *Callizoniceras*, it is instructive to compare this specimen with the example of *Callizoniceras* (*Wollemanniceras*) *keilhacki* (Woll.) from Schwiecheldt, Hanover, illustrated in Pl. 7, figs. 4, 4*a*. Demonstration of a *Callizoniceras*-like final stage in *Epileymeriella* has not been possible hitherto owing to the lack of adult material.

The specimen under discussion was found by the Wright brothers at Leighton Buzzard, but unfortunately not *in situ*. I am unable to comment, therefore, on its stratigraphical position in relation to the *Leymeriella* cf. *hitzeli* recorded by Spath (1924, p. 83) from the A beds of the Speeton Clay. Brinkmann (1937, p. 14) uses *L.* (*E.*) *hitzeli* as an index fossil for an horizon below the main development of *L. regularis*, though still within the broad Regularis Zone of that author.

Distribution. Condensed Tardefurcata-Mammillatum Zones, Arnold's Pit, Billington Crossing, Leighton Buzzard, Beds.; Speeton Clay (Bed A 4), Speeton, Yorkshire.

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THE TRILOBITE *ENCRINURUS MULTISEGMENTATUS* (PORTLOCK) AND ALLIED MIDDLE AND UPPER ORDOVICIAN SPECIES

by R. P. TRIPP

ABSTRACT. An *Encrinurus multisegmentatus* species-group is defined. The main diagnostic criterion is the arrangement of the tubercles on the cranidium; a system of notation is used to indicate the positions of the main glabellar tubercles. *E. multisegmentatus* (Portlock) from the Killey Bridge Beds, Tyrone, is redescribed, and the Middle and Upper Ordovician species which constitute the group are discussed. One new species, *E. lamonti* from the Lower Drummuck Group, Ayrshire, is established.

INTRODUCTION

THE terminology used in this paper is essentially that of Warburg (1925, pp. 1–7) except that the pleurae (ribs) of the pygidium are considered to be marked off by the interpleural, not the pleural, furrows. Temple (1956, pp. 423–4) has shown that the area between the preglabellar furrow and the facial sutures in the encrinurids is homologous with the anterior border of the cranidium in the other members of the Cheiruracea; this area is here referred to as the false preglabellar field. The quoted length of a part is the distance measured parallel to the median line between its extremities; the width is the corresponding measurement at right angles to the median line.

Previous research. There has been little progress in the study of the interrelationships of the species of *Encrinurus* since Reed's paper of 1928. Reed recognized six morphological groups, the fourth of which he defined as follows.

> Pygidium with numerous rings on axis, of which the anterior rings are complete, but the posterior ones are interrupted or weakly marked in the middle. Cephalon with glabella coarsely tuberculated; lateral lobes nodular. Example: *E. multisegmentatus* Portl. Range: Upper Ordovician.

Reed regarded his fourth group as ancestral to his fifth, typified by *E. punctatus* (Wahlenberg), and this view is supported here. Rosenstein (1941) has drawn attention to the regularity of the arrangement of the tubercles in the cranidium of *E. punctatus*.

Definition of the E. multisegmentatus *species-group.* Reed's fourth group included a number of species which are not closely related to each other. The following is a definition of a restricted *E. multisegmentatus* group:

Cephalon coarsely tuberculate; main glabellar tubercles symmetrically arranged in transverse or arcuate rows. False preglabellar field separated from glabella by a broad furrow and itself parted by a well-defined median furrow, with four large tubercles on each side. Pygidium composed of twenty-five or more axial rings and eleven to fourteen pairs of pleurae. Occurrence: Middle and Upper Ordovician, Europe, and North America.

[Palaeontology, Vol. 1, Part 1, 1957, pp. 60–72, pls. 11–12]

System of notation applied to glabellar tubercles. As stated above, the main glabellar tubercles are symmetrically arranged in the *E. multisegmentatus* group, and they are distributed according to different patterns in each species. These main tubercles occur in transverse or arcuate rows, which are numbered I to VII starting from the back. Rows I, II, and III are opposite the posterior, middle, and anterior lateral glabellar lobes respectively; the remaining rows are situated on the frontal lobe. Tubercles which occur between the transverse rows are symbolized by the small roman numeral of the row in front. Pairs of tubercles are numbered in arabic numerals distally from the centre line, for example, IV–1 indicates the pair of tubercles nearest the centre line in the fourth row counted from the back forwards; when necessary left and right tubercles of a pair are distinguished by the suffix L or R. A median tubercle is denoted 0. In recording the formula for a species, regular tubercles which are not always present are placed in parentheses. Supernumerary tubercles, often asymmetrically arranged, are referred to as adventitious and are not numbered. Text-fig. 1 is a diagrammatic representation of the distribution of the main tubercles in certain of the species discussed.

Acknowledgements. I am greatly indebted to Dr. J. T. Temple and Professor W. F. Whittard whose suggestions have added greatly to the value of this work. I have much pleasure in expressing gratitude to the following for the loan of specimens: Dr. W. T. Dean, British Museum (Natural History), London (BM); Professor T. N. George and Dr. E. D. Currie, Hunterian Museum, Glasgow (HM); Dr. G. Henningsmoen, Palaeontological Museum, Oslo (PM); Mr. J. D. D. Smith, Geological Survey and Museum, London (GSM); Professor Alwyn Williams, Queen's University, Belfast; Mr. R. B. Wilson, Geological Survey of Great Britain (Scottish Office) (GSE). The initials following the name of an institution are those subsequently used in referring to particular specimens. Figured specimens collected by the author have been presented to the Hunterian Museum, Glasgow.

DESCRIPTION OF SPECIES

Encrinurus multisegmentatus (Portlock)

Plate 11, figs. 6–8; Plate 12, figs. 1–6

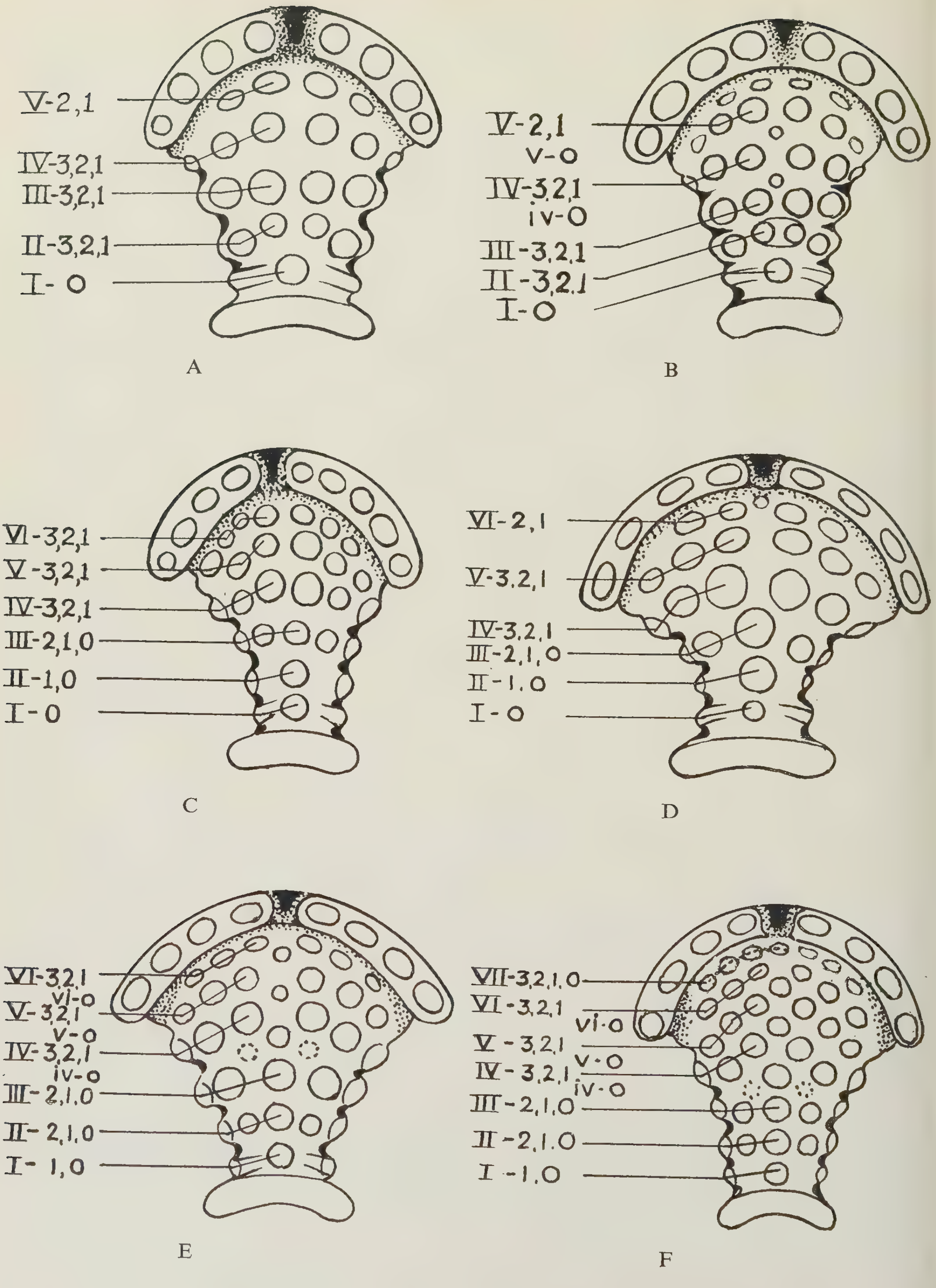
Amphion multisegmentatus Portlock 1843, p. 291, pl. 3, figs. 6*a*, *b*.
Ampyx baccatus Portlock 1843, p. 262, pl. 3, fig. 11.

Diagnosis. Cranidium gently convex longitudinally; glabella elongate, depressed posteriorly; frontal lobe approximately half length of glabella. Tubercle formula: I–0; II–0, 1; III–0, 1, 2; (iv–0); IV–V–VI–1, 2, 3. Fixed cheeks strongly tuberculate, with two conspicuously large tubercles one behind the other.

Horizon and locality. Killey Bridge Beds, Desertcreight, Tyrone, Northern Ireland.

Holotype. GSM 35416 (pygidium). Pl. 12, fig. 4.

Other material. 3 cranidia; 5 pygidia.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III-3,2,1
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I-0
A
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iv-0
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I-0
B
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V-3,2,1
IV-3,2,1
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II-1,0
I-0
C
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v-0
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iv-0
III-2,1,0
II-2,1,0
I-1,0
F

Dimensions

	Holotype	*GSM 35415*
Median length of cranidium	. .	10·6 mm.
Length of glabella	. .	7·5 mm.
Width across false preglabellar field . .	. .	8·8 mm.
Width of glabella across basal lobes . .	. .	3·1 mm.
Length of pygidium.	11·7 mm.	. .
Width of pygidium	11·8 mm.	. .

Description of cranidia. GSM 35415 (Pl. 11, fig. 6; Pl. 12, figs. 2*a*, *b*)—internal mould of incomplete cranidium, holotype of *Ampyx baccatus* Portlock. Cranidium semicircular in outline; glabella and false preglabellar field elongated towards the left; fixed cheeks moderately swollen; fixigenal spines not preserved. Glabella elongate, subpyriform, longitudinal convexity weak, transverse convexity strong at back, weak anteriorly. Frontal lobe strongly expanded, elliptical, extending for approximately half length of glabella. Lateral lobes represented by swellings on lateral slopes of glabella, posterior pair consisting of narrow ridges reaching to a median tubercle. Lateral furrows deep and broad, almost continuous across glabella. Occipital ring short and strongly convex. Apodemes, pointing inwards, near extremities of lateral and occipital furrows, anterior pair the weakest. Axial furrows narrow and deep; large anterior pits immediately behind facial sutures. False preglabellar field separated from glabella by a well-defined furrow, and divided by a deeper furrow offset towards left side. Fixed cheeks moderately convex, rising higher than glabella at back, broad and flattened distally and sloping outwards. Posterior borders short, transverse proximally, bending gently backwards beyond mid-width; posterior border furrows well defined. Cranidium bears dome-shaped tubercules. A median tubercle, I–0, between basal lateral ridges; tubercles II–1 and III–2, which surmount the middle and anterior lateral lobes respectively, are relatively small; three rows of six tubercles on the frontal lobe, tubercles IV–1 large, VI–2, 3 small. Four tubercles on left side of false preglabellar field, five on the extended right side. Occipital ring smooth. Fixed cheeks with scattered small tubercles on inner slopes, and larger tubercles on posterolateral slopes; a large tubercle on summit of

EXPLANATION OF TEXT-FIG. 1

Arrangement of main glabellar tubercles in certain species of the *E. multisegmentatus* group.

A. *Encrinurus praecursor* Tripp, Craighead (Kiln) mudstones, Craighead, after HM A. 4090a, b (Pl. 11, fig. 1).

B. *Encrinurus praecursor* Tripp, Craighead (Kiln) mudstones, Craighead, after HM A. 4091 (Pl. 11, fig. 3).

C. *Encrinurus multisegmentatus* (Portlock), Killey Bridge Beds, Tyrone, after GSM 35413 (Pl. 11, fig. 6).

D. *Encrinurus lamonti* sp. nov., Lower Drummuck Group, New Dailly, after the holotype (Pl. 11, fig. 9).

E. *Encrinurus* aff. *trispinosus* Reed, Lower Drummuck Group, New Dailly, after HM A. 4097a, b (Pl. 11, fig. 12).

F. *Encrinurus trispinosus* Reed, Upper Drummuck Group, Ladyburn, after HM A. 970.

Owing to the strong transverse convexity of the glabella, the lateral tubercles in rows I to IV are only seen in side view.

cheeks opposite middle lateral glabellar lobes, encircled by a broad, shallow, pitted area; another large tubercle placed in front.

BM In. 51476 (Pl. 11, fig. 7; Pl. 12, fig. 1)—internal mould of cranidium. Differs from foregoing specimen chiefly in that glabella is swollen near base of frontal lobe and longitudinal convexity is stronger at front; a small median tubercle, iv–0, is present; row VI is composed of eight small tubercles. There are eight tubercles on the false preglabellar field, four on each side of the median furrow. Fixigenal spines are long, stout, and rounded, directed backwards and gently outwards; four tubercles on border at base of right spine.

GSM 35421, 35420 (Pl. 11, fig. 8)—internal and fragmentary external moulds of a cranidium. Frontal lobe strongly swollen. A large tubercle intercalated between V–1L and VI–1L paired with a minute tubercle on the right side; the occurrence of these

EXPLANATION OF PLATE 11

The photographs are of natural internal moulds unless otherwise stated. The specimens were coated with ammonium chloride before being photographed.

Figs. 1–5. *Encrinurus praecursor* Tripp. 1, HM A. 4090a, ×3. Cranidium with no adventitious tubercles. Craighead (Kiln) mudstones, Craighead. 2, GSE 11732, ×4. Cranidium with tubercles II–1 joined at the base; three small adventitious tubercles anterior to row V are present. Rubber latex cast from external mould. Mudstones at Trochraigue. 3, HM A. 4091, ×4. Cranidium with tubercles iv–0, v–0 and three small adventitious tubercles anterior to row V present. Craighead (Kiln) mudstones, Craighead. 4, HM A. 4092, ×6. Cranidium showing coalescence of tubercles II–1 at the base. External mould. Craighead (Kiln) mudstones, Craighead. 5, HM A. 4093b, ×6. Cranidium showing coalescence of tubercles II–1 and III–1 at the base; four small adventitious tubercles anterior to row V present. External mould. Craighead (Kiln) mudstones, Craighead.

Figs. 6–8. *Encrinurus multisegmentatus* (Portlock). Killey Bridge Beds, Desertcreight, Tyrone, Northern Ireland. 6, GSM 35415, ×2½. Cranidium figured by Portlock (1843) pl. 3, fig. 11) as *Ampyx baccatus*. Note regularity of the tuberculation except for the extra (fifth) tubercle on the right side of the false preglabellar field. 7, BM In. 51476, ×5. Cranidium possessing tubercle iv–0. 8, GSM 35421, ×4. Cranidium with glabella strongly swollen in front.

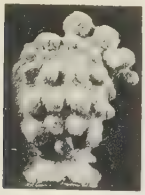
Figs. 9–11. *Encrinurus lamonti* sp. nov. Lower Drummuck Group, east brow of Quarrel Hill, New Dailly, Ayrshire, Scotland. 9, HM A. 4094a, ×5. Holotype, cranidium. 10, HM A. 4095, ×5. Cranidium. 11, HM A. 4096a, ×6. Cranidium.

Figs. 12–14. *Encrinurus* aff. *trispinosus* Reed. Lower Drummuck Group, East Brow of Quarrel Hill, New Dailly, Ayrshire, Scotland. 12, HM A. 4097a, ×4. Cranidium with a large tubercle iv–0 and a pair of small adventitious tubercles alongside. 13, HM A. 4098, ×4. Cranidium showing arrangement of small adventitious tubercles in circlets around tubercles III–0 and IV–3L. 14, HM A. 4099 (Begg Collection), ×2½. Large Cranidium.

Figs. 15–19. *Encrinurus trispinosus* Reed. Starfish Bed, Upper Drummuck Group, Ladyburn, Ayrshire, Scotland. 15, BM In. 23215 (Gray Collection), ×4. Cranidium with sparse tuberculation, and tubercle iii–0 present; tubercles II–0 and III–0 are replaced by paired tubercles; row VII is lacking. 16, BM In. 46812 (Gray Collection), ×3. Cranidium bearing large tubercles; abnormal in that iv–0 is exceptionally large, and v–0 is lacking. 17, BM In. 23226 (Gray Collection), ×2. Cranidium and thoracic segments, showing axial spines on fifth and seventh rings and pleural spines on sixth segment; five tubercles in rows I, II, and III, tubercle iv–0 large and in line with IV–2, 3. Rubber latex cast from external mould. 18, BM In. 46834 (Gray Collection), ×3. Cranidium with tubercle iv–0 lacking. Rubber latex cast from external mould. 19, HM A. 4002 (Lamont Collection), ×3½. Cranidium bearing small, closely spaced tubercles; seven tubercles in row III and row VII well developed. Rubber latex cast from external mould.

Fig. 20. *Encrinurus laurentinus* Twenhofel. Ellis Bay Formation, Junction Cliff, Anticosti Island. BM In. 19807, ×2½. Cranidium showing large VII–0 tubercle.

PLATE 11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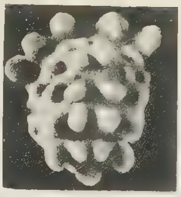
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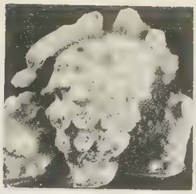
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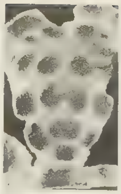
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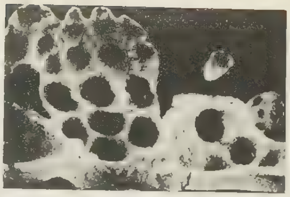
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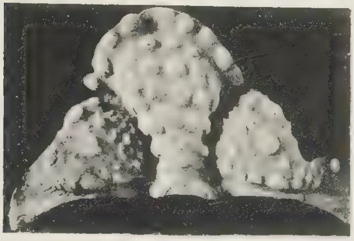
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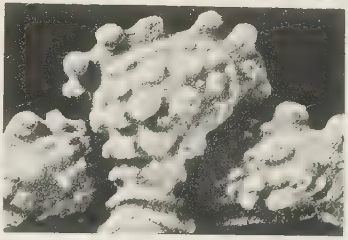
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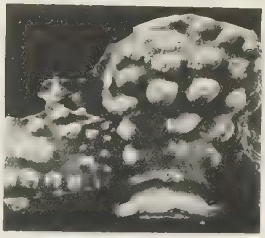
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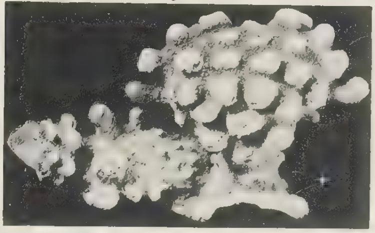
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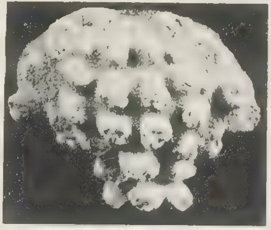
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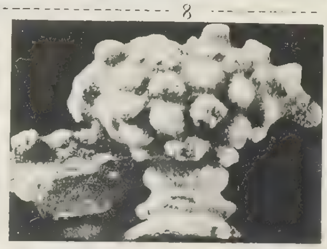
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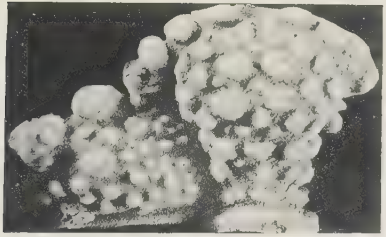
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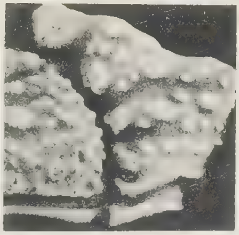
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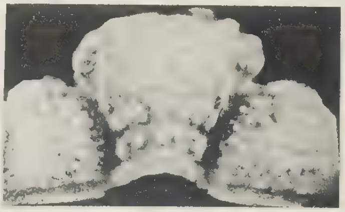
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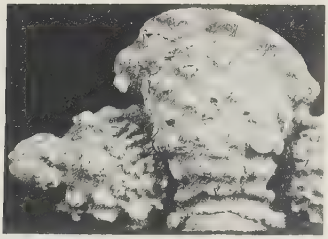
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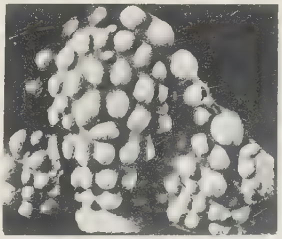
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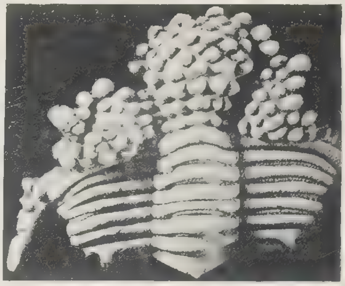
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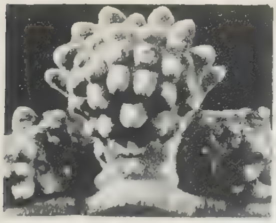
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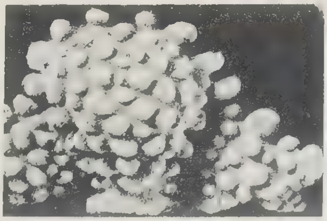
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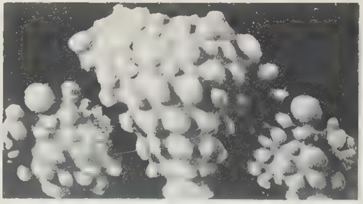
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TRIPP, *Encrinurus*

tubercles may indicate the inception of a new row. Four tubercles on the right side of the false preglabellar field on the external mould; left side not preserved. Surface of tubercles and cheeks granular.

Description of pygidia. Holotype, GSM 35416 (Pl. 12, fig. 4)—internal mould of pygidium. Pygidium six-sevenths as long as wide. Axis one-quarter anterior width of pygidium, narrowing slowly and steadily backwards, imperfectly preserved at front and back; eleventh to twentieth rings distinct laterally, apparently rubbed mesially. Axial furrows moderately deep anteriorly, dying out posteriorly. Postaxial ridge short, flanked by a narrow ridge on left side. Pleural regions gently convex; anterior half-pleurae moderately swollen. Thirteen pairs of pleurae, last pair weakly developed and only one-sixth length of pygidium. Pleurae strongly raised, widening only slowly towards sides, apparently terminating in short free points; anterior pleurae directed outwards and slightly backwards at first, bending downwards and backwards at fulcrum; successive pleurae run more obliquely backwards, hindmost pair subparallel. Interpleural furrows deeply impressed.

GSE 11731 (Pl. 12, fig. 3)—external mould of pygidium. Length two-thirds width of pygidium. Axis one-fifth anterior width of pygidium; thirty axial rings, axial furrows posterior to fifteenth faint, becoming obsolete mesially; third and fourth rings incompletely developed. Thirteen pairs of pleurae. Surface minutely granular, with a row of larger granules along posterior margins of pleurae.

BM In. 51477 (Pl. 12, fig. 5)—internal mould of pygidium, with portion of test preserved at back. Axial rings thirty-two in all, faintly continuous on internal mould, strongly discontinuous on test. Postaxial ridge long and narrow, partially fused with posterior pair of pleurae. Abnormal in that right pleural region is shorter than left and composed of twelve, compared with thirteen, pleurae.

GSM 35417 (Pl. 12, fig. 6)—internal mould of pygidium. Pleural regions bent strongly downwards at fulcrum. Pleurae widen markedly towards sides. Twelfth pair of pleurae meet at posterior tip of pygidium, enclosing the short postaxial ridge.

GSM 35419—internal mould of pygidium. Twelve pairs of pleurae present.

BM In. 51540—external cast of pygidium. Twelve pairs of pleurae present.

Remarks. It is unfortunate that the fine cranidium which Portlock figured is deformed, having five tubercles on the right side of the false preglabellar field; no other specimen belonging to the species-group has been noticed with this abnormality. Despite numerous records of *E. multisegmentatus* from various localities, the only authentic specimens known are those described above, all from the Killey Bridge Beds.

Encrinurus praecursor Tripp

Plate 11, figs. 1–5

Encrinurus praecursor Tripp 1954, p. 681, pl. 4, figs. 13–25.

Diagnosis. Glabella broad posteriorly, strongly convex; frontal lobe not more than half length of glabella. Tubercle formula: I–0; II–III–1, 2, 3; (iv–0); IV–1, 2, 3; (v–0); V–1, 2. Fixed cheeks sparsely tuberculate, with two large tubercles one behind the other.

Horizon and locality. Craighead (Kiln) mudstones (Lower Caradocian), Craighead Quarry, and mudstones at Trochraigue, Ayrshire, Scotland.

Remarks. There is little variation in the arrangement of the first three rows of tubercles; the adventitious tubercle alongside I–0 previously figured (Tripp 1954, pl. 4, fig. 14) is unique. However, tubercles II–1 and III–1 are occasionally joined near the base (Pl. 11, figs. 2, 4, 5), an important point suggesting comparison with the single median tubercle in these rows in other members of the group. The median tubercle v–0, though small, occurs in over half the forty specimens studied. There is great variation in the occurrence of the small tubercles anterior to row V (Pl. 11, figs. 2, 3, 5), but these tubercles are too irregular to be considered as other than adventitious.

Encrinurus sp.

Plate 12, figs. 19–21

Horizon and locality. Cyrn-y-brain Beds, 150 yards north-east of Plâs-uchaf, Denbighshire, N. Wales.

EXPLANATION OF PLATE 12

The photographs are of natural internal moulds unless otherwise stated. The specimens were coated with ammonium chloride before being photographed.

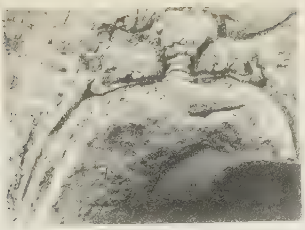
Figs. 1–6. *Encrinurus multisegmentatus* (Portlock). Killey Bridge Beds, Desertcreight, Tyrone, Northern Ireland. 1, BM In. 51476, ×1½. Cranidium; see Pl. 11, fig. 7. 2*a*, *b*, GSM 35415, ×2½. Cranidium, frontal and lateral views; see Pl. 11, fig. 6. 3, GSE 11731, ×4. Pygidium showing granulation and incomplete development of third and fourth axial rings. Rubber latex cast from external mould. 4, GSM 35416, ×2½. Holotype, pygidium. Figured by Portlock (1843, pl. 3, figs. 6*a*, *b*. 5, BM In. 51477, ×2½. Pygidium with long postaxial ridge; abnormal in that there are twelve pleurae on the right side and thirteen on the left. The test is preserved at the back; note discontinuous axial rings. 6, GSM 35417, ×2½. Pygidium with twelve pairs of wide pleurae.

Figs. 7–10. *Encrinurus lamonti* sp. nov. Lower Drummuck Group, east brow of Quarrel Hill, New Dailly, Ayrshire, Scotland. 7*a*, *b*, HM A. 4094a, ×5. Holotype, cranidium, frontal and lateral views. 8, HM A. 943b (Lamont Collection), ×4. Right free cheek. Rubber latex cast from external mould. 9, HM A. 4100, ×6. Pygidium showing the row of granules along margins of pleurae. Rubber latex cast from external mould. 10, HM A. 4101a, ×4. Pygidium with paired axial tubercles.

Figs. 11–17. *Encrinurus trispinosus* Reed. Starfish Bed, Upper Drummuck Group, Ladyburn, Ayrshire, Scotland. 11, BM In. 41279 (Gray Collection), ×3. Cranidium and thoracic segments; note pair of small tubercles alongside tubercle iv–0. Rubber latex cast from external mould. 12, BM In. 41402 (Gray Collection), ×2. Cranidium with a pair of large tubercles alongside, tubercle iv–0 and tubercle IV–1L divided. 13, BM In. 46867 (Gray Collection), ×3. Enrolled dorsal shield; lateral view. Rubber latex cast from external mould. 14, BM In. 46842 (Gray Collection), ×2. Pygidium with fourth and fifth right pleurae joined proximally. Rubber latex cast from external mould. 15, HM A. 4011 (Lamont Collection), ×3. Pygidium showing granulation. External mould. 16*a*, *b*. HM A. 4103 (Lamont Collection), ×2½. Narrow pygidium with fifth and sixth pleurae joined distally; dorsal and lateral views. 17, HM A. 4003a (Lamont Collection), ×3½. Broad pygidium.

Fig. 18. *Encrinurus* sp. *Tretaspis* Shales, road section south of Lunner, Hadeland, Norway. PM 35059 Holtedahl Collection), ×3. Pygidium with test partly preserved, figured by Størmer (1945, pl. 2, fig. 14) as *E. laurentinus.*

Figs. 19–21. *Encrinurus* sp. Cyrn-y-brain Beds, 150 yds. north-east of Plâs-uchaf, Denbighshire, North Wales. 19, GSM LW 1098, ×3. Right free cheek. 20, GSM LW 1096, ×2½. Cranidium. Rubber latex mould from external cast. 21, GSM LW 1096, ×2. Pygidium with eleventh and twelfth left pleurae joined near base; closely associated with cranidium.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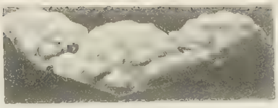
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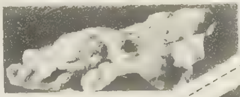
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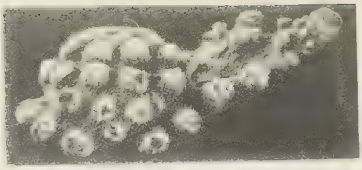
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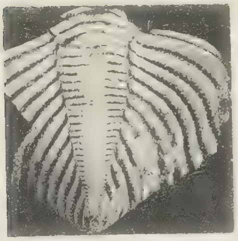
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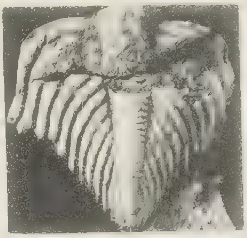
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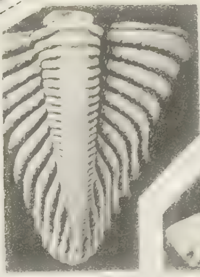
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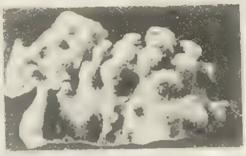
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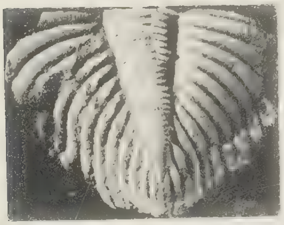
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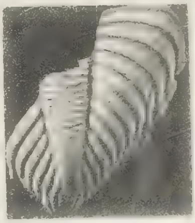
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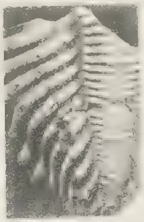
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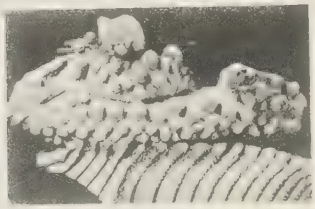
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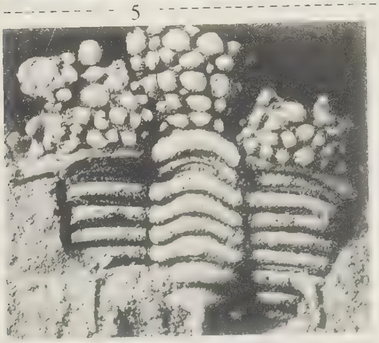
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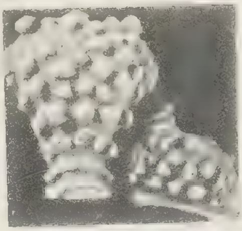
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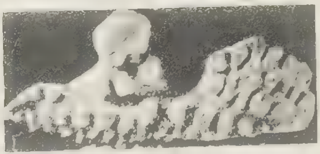
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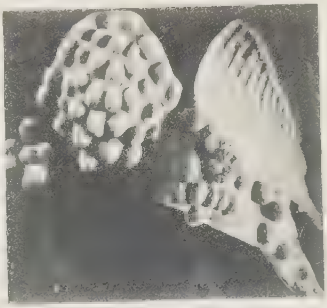
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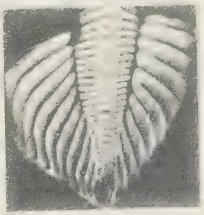
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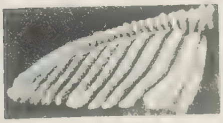
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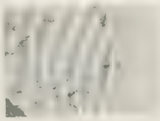
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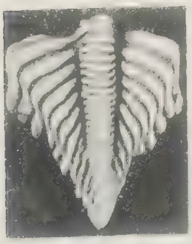
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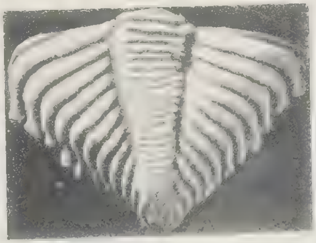
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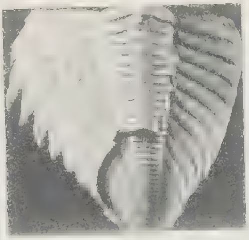
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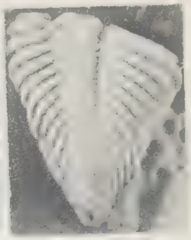
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TRIPP, *Encrinurus*

Material. Incomplete external mould of cranidium and associated internal mould of pygidium; 1 free cheek.

Description. Glabella elongate and pointed anteriorly, gently convex longitudinally and transversely. Frontal lobe long and narrow; posterior part of glabella not preserved. False preglabellar field separated from glabella by a narrow furrow, and divided by a broad median furrow. Fixed cheeks narrow, strongly convex, Palpebral lobes stout, situated close to glabella; palpebral furrows shallow and broad. Lateral borders broad; fixigenal spines short, broad-based, directed backwards and gently outwards. Cranidium bears large, rounded tubercles arranged as follows: III–0, 1, 2; IV–V–VI–1, 2, 3; VII–1, 2. Four tubercles on each side of false preglabellar field. Fixed cheeks coarsely tuberculate; one large tubercle opposite palpebral lobe, and another in front of it; a row of small tubercles just above base of palpebral lobe. A few tubercles near base of genal spines.

Eye stalks stout, with scattered tubercles at base. Free cheeks narrow, with three tubercles in inner area. Pseudoglabellar areas large, tubercles three deep. Lateral borders narrow; one main row of tubercles, decreasing in size away from axial furrow, and a few smaller, scattered tubercles.

Pygidium longer than wide. Axis one-quarter anterior width of pygidium, axial rings faintly continuous; postaxial ridge one-eighth length of pygidium. Axial furrows deep and broad at front, becoming faint posteriorly. Pleural lobes strongly convex, composed of thirteen pairs of pleurae; eleventh and twelfth left pleurae joined near base. Interpleural furrows relatively shallow.

Encrinurus trispinosus Reed

Plate 11, figs. 15–19; Plate 12, figs. 11–17

Encrinurus multisegmentatus Reed 1906, p. 122, pl. 16, figs. 9–11*a*.
Encrinurus multisegmentatus var. *trispinosus* Reed 1914, p. 39, pl. 7, figs. 1–3.
Encrinurus multisegmentatus var. *girvanensis* Reed 1935, p. 50, pl. 4, fig. 9.

Diagnosis. Glabella subpentagonal, moderately convex; frontal lobe about four-sevenths length of glabella. Tubercle formula: I–0, 1; II–0, 1, 2; (iii–0); III–0, 1, 2; iv–0; IV–1, 2, 3; v–0; V–1, 2, 3; vi–0; VI–1, 2, 3; (VII–0, 1, 2, 3). Fixed cheeks coarsely tuberculate, with one large tubercle at the front.

Horizon and locality. Starfish Bed, Upper Drummuck Group, Ladyburn, Ayrshire, Scotland.

Remarks. Reed does not state the features which distinguish his subspecies *girvanensis* from *trispinosus*, but he makes no mention of thoracic spines in the description of the former, and it seems that he regarded the absence of spines as the diagnostic character. Certainly, thoracic spines are not distinguishable on the holotype of *girvanensis*, but only the internal mould is preserved, and spines are rarely preserved on internal moulds. A large number of external moulds have been examined, and all show a pair of pleural spines on the sixth segment, a small axial spine on the fifth ring and a large spine on the seventh ring (there is no axial spine on the sixth ring, contrary to Reed's statement).

Even if thoracic spines are occasionally absent, this is not necessarily a matter of taxonomic importance. There is no other significant difference between the holotype of *girvanensis* and specimens referable to *E. trispinosus*, and consequently the two forms are considered synonymous.

The size and arrangement of the glabellar tubercles is much more variable in *E. trispinosus* than in the other species of the group. It is quite common for any of the regular tubercles, particularly the lateral ones (Pl. 11, fig. 19), to subdivide, and adventitious tubercles are frequent. *E. trispinosus* is distinguished in having tubercles on the posterior lateral glabellar lobes; adventitious tubercles occur on about one-third of the specimens between the lateral and median tubercles (Pl. 11, figs. 16, 17, 18), corresponding with the rows in front. The median tubercle iv–0 is rarely absent (Pl. 11, fig. 18); it sometimes occurs between rows III and IV (Pl. 11, fig. 16), but it is often situated anteriorly, displacing tubercles IV–1 towards the front (Pl. 11, figs. 17, 18). This tubercle iv–0 is frequently flanked by a pair of tubercles (Pl. 12, figs. 11, 12) which appear as small, posteriorly placed, adventitious tubercles in the Lower Drummuck form related to this species (Pl. 11, figs. 12, 14). *E. punctatus* has a pair of large tubercles in corresponding positions (Rosenstein 1941, pl. 1, fig. 1). Tubercle v–0 is present in all except one of the specimens of *E. trispinosus* studied (Pl. 11, fig. 16) and tubercle vi–0 is usually present also. Row VII is composed of well-formed tubercles in about half the specimens (Pl. 11, fig. 19), and it often includes a median tubercle, which sometimes occurs alone (Pl. 11, fig. 16). The cranidium figured as Pl. 11, fig. 15 is an unusual variant. The tuberculation is sparse, and the glabella is short and broad posteriorly. It is one of the few specimens possessing tubercle iii–0, and tubercles II–0 and III–0 are replaced by paired tubercles; the tendency towards a quincunxial arrangement might account for this modification, but the arrangement of the tubercles is reminiscent of that in *E. praecursor*.

Encrinurus aff. *trispinosus* Reed

Plate 11, figs. 12–14

Horizon and locality. Lower Drummuck Group, east brow of Quarrel Hill, New Dailly, Ayrshire, Scotland.

Remarks. This form may be closely compared with simple specimens of *E. trispinosus*. It differs from *E. trispinosus* and approaches *E. multisegmentatus* in the less uniform size of the cranidial tubercles, and in the occurrence of a large tubercle on the fixed cheek opposite the palpebral lobe. There is a tendency for small adventitious tubercles to be arranged in a circlet round one of the main tubercles (Pl. 11, fig. 13).

Encrinurus lamonti sp. nov.

Plate 11, figs. 9–11; Plate 12, figs. 7–10

Diagnosis. Glabella broad and inflated anteriorly, strongly convex longitudinally; frontal lobe more than half length of glabella. Tubercle formula: I–0; II–0, 1; III–0, 1, 2; IV–V–1, 2, 3; VI–1, 2. Fixed cheeks sparsely tuberculate, with largest tubercle opposite palpebral lobe.

Horizon and locality. Lower Drummuck Group, east brow of Quarrel Hill, New Dailly, Ayrshire, Scotland.

Holotype. HM A. 4094a, b (cranidium). Pl. 11, fig. 9; Pl. 12, figs. 7*a*, *b*.

Other material. 2 cranidia, 7 free cheeks, 4 pygidia.

Dimensions

	Holotype	*HM A. 4096 a, b*
Median length of cranidium . . .	5·5 mm.	4·8 mm.
Length of glabella	4·4 mm.	3·9 mm.
Width across false preglabellar field . .	6·5 mm.	5·7 mm.
Width of glabella across basal lobes . .	2·3 mm.	2·2 mm.

Description. Cranidium elliptical in outline; fixed cheeks gently swollen; fixigenal spines not preserved. Glabella subrhomboidal, depressed at back, strongly inflated anteriorly. Frontal lobe widely expanded, gently rounded in outline, extending for more than half length of glabella. Lateral lobes represented by swellings on lateral slopes of glabella, posterior pair consisting of faint ridges reaching to a median tubercle. Lateral furrows broad, defined only at sides. Occipital ring short, strongly convex. Apodemes near extremities of lateral and occipital furrows, anterior pair weakly developed. Axial furrows deep; large anterior pits immediately behind facial sutures. False preglabellar field separated from glabella by a shallow furrow, and divided by a broad median furrow, sloping steeply forwards and downwards. Fixed cheeks narrow, strongly convex. Palpebral lobes large and elevated, situated close to glabella and opposite middle lateral furrows; palpebral furrows broad, encircling base of lobes. Posterior borders short, transverse proximally; posterior border furrows well defined. Cranidium bears elongated dome-shaped tubercles. A small median tubercle, I–0, between basal lateral ridges. Small tubercles, II–1 and III–2, surmount the middle and anterior lateral lobes respectively; on the frontal lobe, two rows of six tubercles, IV–V–1, 2, 3, and one row of four, VI–1, 2. Smaller adventitious tubercles, irregularly placed, at the front. Four large tubercles on each side of false preglabellar field. Fixed cheeks sparsely tuberculate; one large tubercle opposite middle lateral lobes, and another opposite anterior lateral furrows. Palpebral lobes with four tubercles near base, and scattered small tubercles above.

Eye stalks slender, with a row of small tubercles near base. Free cheeks narrow, sloping steeply outwards; inner areas sparsely tuberculate. Pseudoglabellar areas large and swollen, with scattered tubercles up to four deep. Lateral and false anterior borders narrow, continuous, weakly convex, narrowing rapidly anteriorly; two rows of tubercles and a few scattered ones outside; posterior inner areas smooth. Border furrows broad and shallow.

Pygidium composed of about thirty-two axial rings and twelve to fourteen pairs of pleurae. Axis one-quarter anterior width of pygidium, narrowing slowly backwards; axial rings barely continuous at back on internal moulds, discontinuous behind the fifth ring on external moulds. Postaxial ridge short. Axial furrows well developed anteriorly, dying out posteriorly. Pleural regions strongly convex; anterior half-pleurae moderately swollen. Pleurae strongly raised, widening little towards sides, terminating in short, free points. Interpleural furrows deeply impressed. HM A. 4101a, b (Pl. 12, fig. 10) shows paired axial tubercles on seventh, eleventh, seventeenth, and twenty-fourth rings, and tubercles on pleurae. A row of granules along anterior and posterior margins of pleurae.

Remarks. Our new species differs from *E. trispinosus* and resembles *E. multisegmentatus* in having no tubercles on the basal lateral lobes, only three tubercles in row II, and no inter-row tubercles. *E. lamonti* resembles the specimen of *E. multisegmentatus* with the swollen frontal lobe (Pl. 12, fig. 8) so closely that the writer was formerly inclined to regard the new form as a subspecies (Tripp 1954, p. 683). Two types of encrinurid free cheek occur in the Lower Drummuck Group; that with sparse tuberculation (Pl. 12, fig. 8) is provisionally attributed to *E. lamonti*, that with strong tuberculation to *E.* aff. *trispinosus*, in accordance with the characters of the fixed cheeks. In this respect *E. lamonti* occupies an intermediate position between *E. praecursor* and *E. trispinosus*. The pygidia referred to *E. lamonti* differ from those included in *E.* aff. *trispinosus* in having the granules restricted to the anterior and posterior margins of the pleurae (Pl. 12, fig. 9), as in *E. praecursor* (Tripp 1954, pl. 4, fig. 18*b*).

Encrinurus laurentinus Twenhofel

Plate 11, fig. 20

Encrinurus laurentinus Twenhofel 1928, p. 328, pl. 59, figs. 2–5.

Diagnosis. Glabella rounded, swollen anteriorly; frontal lobe approximately three-fifths length of glabella; tubercle formula: I–0; II–0, 1; III–0, 1, 2; IV–1, 2, 3; (v–0); V–VI–1, 2, 3; VII–0. Fixed cheeks devoid of large tubercles.

Horizons and localities. English Head (Richmondian) to Ellis Bay (Gamachian) Formation, Anticosti Island, North America.

Remarks. This species bears a closer resemblance to *E. lamonti* than to *E. multisegmentatus*, but differs from both in the shape of the glabella and in the more uniform size of the tubercles on the cranidium. The pygidium from the *Tretaspis* Shales referred to *E. laurentinus* by Størmer (1945, p. 411, pl. 2, fig. 14; this paper, Pl. 12, fig. 18) does not appear to belong to this species, though it may well be a member of the group; pygidial characters alone are not diagnostic. The specimen demonstrates clearly how the furrows are fainter on the external surface than on the internal.

COMPARISON OF THE *E. MULTISEGMENTATUS* GROUP WITH OTHER SPECIES

The character of the false preglabellar field distinguishes the *E. multisegmentatus* group from almost all other known forms. The cranidium from the Slade Beds (SM A. 30718), referred by Reed (1904, p. 387) to *E. multisegmentatus*, has nine tubercles on the false preglabellar field and no median depression, and the same applies to the cranidium from the Estonian Lyckholm Formation, figured as *E.* cf. *multisegmentatus* by Schmidt (1881, pl. 15, figs. 19*a*, *b*, *c*). Both these forms may be distantly related to our group.

The *E. multisegmentatus* group resembles *E. punctatus* (Wahlenberg), the type species of *Encrinurus*, in certain important features. Many Swedish, most British, and apparently all Estonian (Rosenstein 1941, p. 52) specimens of *E. punctatus* have eight tubercles on the false preglabellar field, though the field is not distinctly divided or separated from the glabella. As Rosenstein (1941, p. 55) has shown, the main glabellar tubercles of *E. punctatus* are symmetrically arranged in transverse rows; the pattern is fundamentally similar to that in the *E. multisegmentatus* group, although the shape of the glabella is quite different. It is intended to discuss *E. punctatus* and some other Silurian forms in a subsequent paper.

GENERAL REMARKS

1. The chief diagnostic feature of the *Encrinurus multisegmentatus* species-group lies in the false preglabellar field, which is separated from the glabella by a broad furrow and is itself parted by a well-defined median furrow, with four tubercles on each side.

2. The basic arrangement of the main glabellar tubercles is constant in each species. Adventitious tubercles occur also, and are particularly numerous on some specimens of *E. trispinosus*, in which they are often as large as the main tubercles and indistinguishable from them except in position.

TABLE SHOWING THE BASIC NUMBER OF GLABELLAR TUBERCLES IN EACH TRANSVERSE ROW IN THE SPECIES OF THE *E. MULTISEGMENTATUS* GROUP

row *species*	I	II	III	iv	IV	v	V	vi	VI	VII
E. praecursor Tripp	1	6	6	. .	6	(1)	4	. .	. .	. .
E. multisegmentatus (Portlock) . .	1	3	5	. .	6	. .	6	. .	6	. .
E. lamonti sp. nov.	1	3	5	. .	6	. .	6	. .	4	. .
E. laurentinus Twenhofel	1	3	5	. .	6	. .	6	. .	6	1
E. sp., Cyrn-y-brain Beds	?	?	5	. .	6	. .	6	. .	6	4
E. aff. *trispinosus* Reed	3	5	5	1	6	(1)	6	. .	6	. .
E. trispinosus Reed	3	5	5	1	6	1	6	1	6	(7)

Rows I, II, and III occur opposite the posterior, middle, and anterior lateral lobes respectively; the remaining rows are situated on the frontal lobe.

3. There is a marked gradation in the arrangement of the glabellar tubercles in the species discussed. *E. praecursor* is distinguished by having six tubercles in rows II and III, but the partial fusion of the two middle tubercles in some specimens (Pl. 11, fig. 5) indicates their equivalence to the single median tubercle in these rows in the other members of the group. *E. multisegmentatus*, *E. lamonti*, and *E. laurentinus* are almost identical in the arrangement of the glabellar tubercles; *E. trispinosus* is much more complex.

4. The density of tuberculation on the fixed and free cheeks differs considerably both between specimens of the same species (Pl. 11, figs. 15 and 17) and between different species. One or two tubercles on the fixed cheeks are much larger than the rest, except in *E. laurentinus*.

5. The thorax is known only in *E. trispinosus* and in one specimen of *E. praecursor*. In both forms there are spines on the fifth and seventh axial rings, and on the sixth pair of the pleurae.

6. The pygidium is distinguished by the large number of axial rings and pairs of pleurae which it carries. The rings are faintly continuous on the internal surface, but become discontinuous posteriorly on the external surface (Pl. 12, fig. 18). Within specific limits pygidia vary in relative proportions (Pl. 12, figs. 16*a*, 17), in numbers of pairs of pleurae (Pl. 12, figs. 4, 5, 6), and in possession of axial tubercles (Pl. 12, fig. 10; Twenhofel 1928, pl. 49, fig. 3; Tripp 1954, pl. 4, fig. 24). There is a tendency for adjacent pleurae to unite (Pl. 12, figs. 14, 16, 21; Tripp 1954, pl. 4, fig. 22).

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SUBTERRANIPHYLLUM, A NEW TERTIARY CALCAREOUS ALGA

by G. F. ELLIOTT

ABSTRACT. A distinctive coarse-celled branching coralline alga, characteristic of the Oligocene of the Mediterranean and Middle East, is described as *Subterraniphyllum thomasi* gen. et. sp. nov. and briefly discussed.

THE branching corallines, of which the familiar little *Corallina officinalis* Linn. is a Recent example, are common fossils in the Tertiary, being represented usually by the dissociated segments, which come apart after the death of the plant. Whilst genera such as *Corallina*, *Amphiroa*, and *Jania* are normally readily distinguishable, they range from Eocene to Recent, and species are difficult to distinguish for dating purposes. The form described below possesses a more restricted range, differs conspicuously from the genera named, and has proved of service in dating Tethyan Tertiary rocks in the Mediterranean and Middle East.

Family CORALLINACEAE

Subfamily CORALLINAEA

Genus SUBTERRANIPHYLLUM gen. nov.

Diagnosis. Branching segmented coralline alga, differing from other genera of the subfamily in the distinctive very coarse and irregular cell-mesh of the medullary tissue; conceptacles not seen. Type species *S. thomasi* sp. nov.

Subterraniphyllum thomasi sp. nov.

Plate 13

Dendrophyllum cf. *gurgurdanensis* Thomas MS., Van Bellen 1956, pl. 2, figs. *b*, *c* (no description).

Description. Coralline segments about 1·5 mm. long by 0·75 mm. maximum diameter, bead-like in form, circular in cross-section, ends rounded: a minority of segments show incipient bifurcation. Medullary tissue with coarse irregular cell-mesh: narrow perithallial zone with a much finer, regular, mesh. In vertical section the medullary cells are seen to be about 0·117 mm. high by 0·078 mm. wide: the upper and lower limits of cell-rows are parallel and regularly transverse, but the lateral walls are irregularly set both within and as between different rows. They are straight or curved and only rarely parallel, so giving rise to rows of irregular-trapezoid cells. Laterally they pass by a narrow transition-zone of irregular curved cells into a fine bonded-brick pattern of small rectangular perithallial cells, about 0·015 mm. by 0·010 mm. In transverse section

[Palaeontology, Vol. 1, Part 1, 1957, pp. 73–75, pl. 13]

the medullary tissue shows as a clear central mesh of irregular-polygonal cells, bordered by a narrow well-defined marginal zone of two to three rows of perithallial cells. In thin section the cell-wall material, especially that of the perithallial tissue, appears almost black, more so than in other corallines, and this feature is distinctive.

Holotype. The specimen figured in Pl. 13, fig. 5; Persia, Gach Saran Well 10, depth 4,725–6 ft.; about the middle of the Rupelian (Middle Oligocene). Brit. Mus. (Nat. Hist.) Dept. Pal. reg. no. V. 34628.

Paratypes. The specimens figured in Pl. 13, figs. 2, 3, 4, 9; same locality and geological horizon as the holotype, well-depths 4,723–6 ft. Brit. Mus. reg. nos. V. 34628, V. 34629.

Geological horizon. Locally abundant at different horizons throughout the Tethyan Oligocene (Lattorfian to Chattian) of the Mediterranean and Middle East. Known less commonly from the Upper Eocene and Aquitanian (basal Miocene) of Sicily and from the Aquitanian of Persia, but only of common occurrence in the Oligocene (e.g. the subsurface Oligocene of Kirkuk, Iraq; Van Bellen 1956).

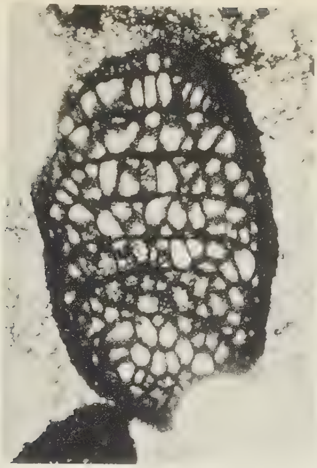
Remarks. This fossil was first noted as stratigraphically useful by Mr. A. N. Thomas in his studies of the Persian Asmari Limestone (Thomas 1950, 1952) but no account was published by him. In unpublished reports it has often been mentioned under manuscript names, and was figured as *Dendrophyllum* cf. *gurgurdanensis* Thomas MS. by Van Bellen (1956). The opportunity is now taken to dedicate the species to Mr. Thomas, in recognition of his work on Persian micropalaeontology.

Material examined from Sicily, Iraq, Persia, and Oman shows some small variation in segment- and cell-size, but not more than one might expect from such a coralline alga, and it does not suggest subdivision of the species either in its vertical range or horizontal distribution.

My thanks are offered to Mr. Thomas, who generously ceded me his publication-priority over this species, and to Dr. F. E. Eames of British Petroleum for information on its different occurrences and helpful discussion of this and other corallines; similarly to Dr. A. H. Smout of Iraq Petroleum, and to the chief geologists and managements of British Petroleum Co., Ltd., and Iraq Petroleum Co., Ltd., for permission to publish this note.

EXPLANATION OF PLATE 13

Figs. 1–9. Thin sections of segments of *Subterraniphyllum thomasi* sp. nov., ×50: nos. 2, 3, 4, 5, and 9 from the Middle Oligocene of Gach Saran Well No. 6, Persia, 4,723–6 ft.: nos. 1 and 6 from the Oligocene of Falaij, Oman, Arabia: nos. 7 and 8 from the Oligocene of Tawi Silaim, Oman. 1, Oblique-transverse section; Brit. Mus. (Nat. Hist.), Dept. Pal. reg. no. V. 34630. 2, Oblique section of bifurcating segment, reg. no. V. 34628. 3, Transverse section, reg. no. V. 34629. 4, Vertical section of incomplete segment, reg. no. V. 34629. 5, Vertical section of nearly complete segment: holotype, reg. no. V. 34628. 6, Oblique transverse section, reg. no. V. 34630. 7, Near-vertical section of bifurcating segment, reg. no. V. 34631. 8, Transverse section, reg. no. V. 34631. 9, Vertical section of curved segment, reg. no. V. 34629.



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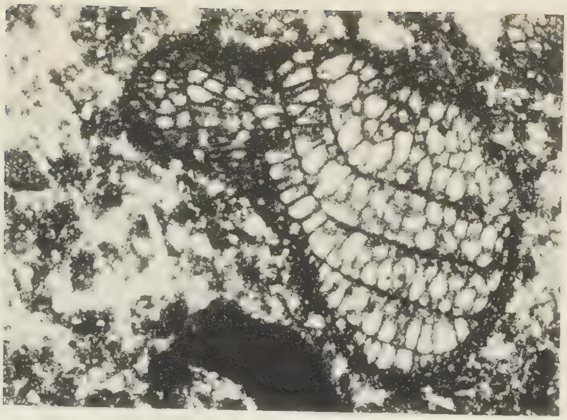

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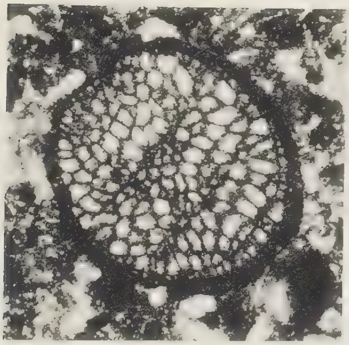

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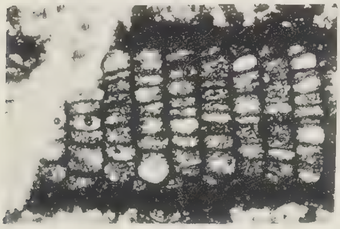

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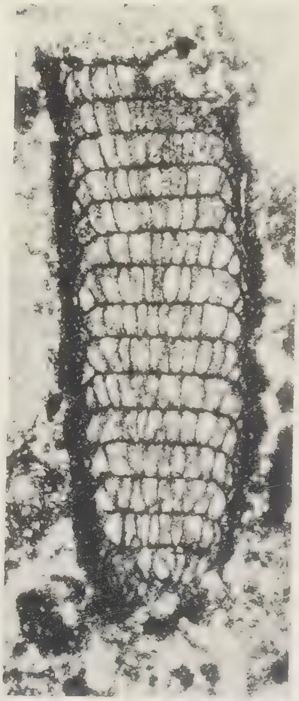

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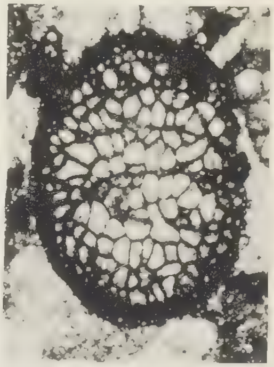

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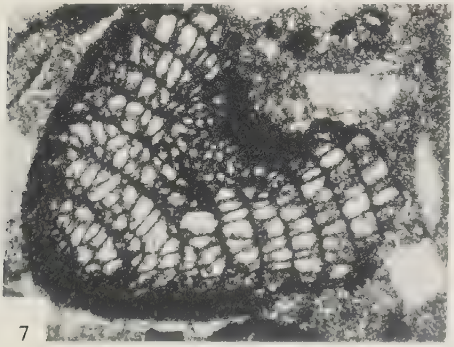

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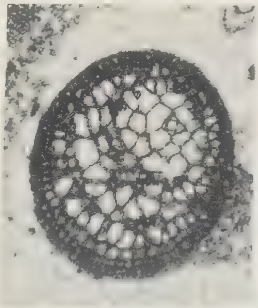

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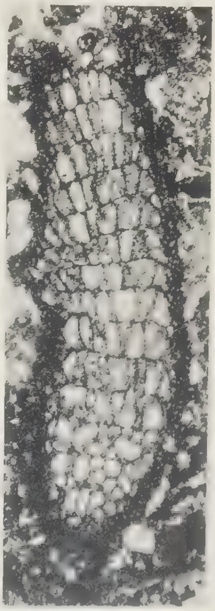

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ELLIOTT, *Subterraniphyllum*

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THE DISTRIBUTION OF THE FORAMINIFER *ALLIATINA EXCENTRICA* (DI NAPOLI ALLIATA) AND THE NEW GENUS *ALLIATINELLA*

by D. J. CARTER

ABSTRACT. *Alliatina excentrica* (di Napoli Alliata) is recorded for the first time from the Pliocene of the Anglo-Belgian basin. The distribution of *A. excentrica* and *Alliatinella gedgravensis* in the Pliocene of Europe, and the genus *Alliatina* in Recent seas is considered. It is concluded that *A. excentrica* is a warm-water species characteristically inhabiting shallow ,sub-littoral environments, and its disappearance from the Anglo-Belgian basin marks the Plio-Pleistocene boundary. The type species of *Alliatinella* is described and figured, and the genus defined. The relationship of *Alliatinella* to *Alliatina* and *Cushmanella* is discussed.

DISTRIBUTION

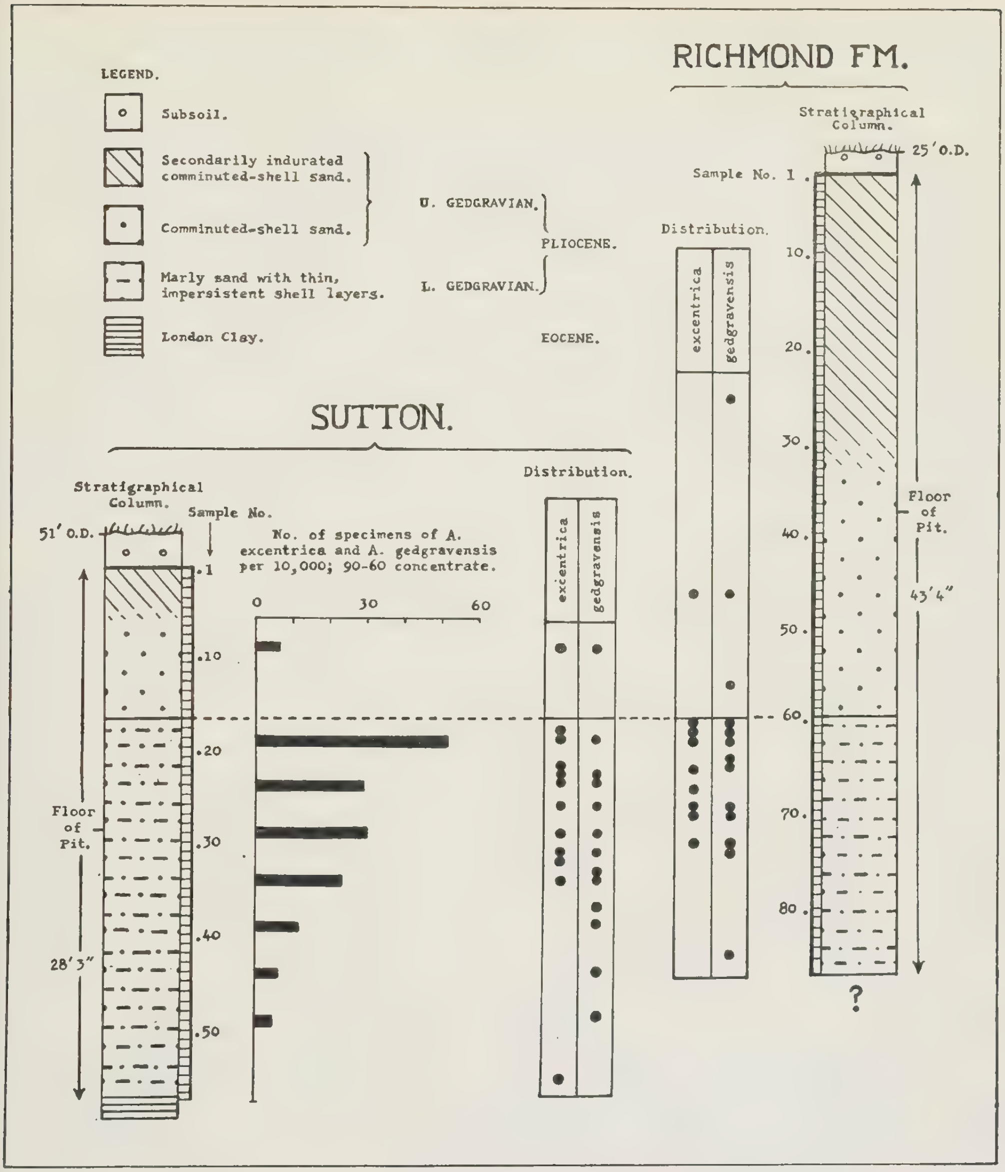
THE foraminifer *Alliatina excentrica* (di Napoli Alliata) has been found to be widely, but sparsely, distributed in the Gedgravian (Coralline Crag) of East Anglia. It is associated with a closely related, hitherto undescribed species, here designated *Alliatinella gedgravensis* gen. and sp. nov. Since *A. excentrica* has previously been recorded only from the Upper Pliocene 'Astian' of Italy (Napoli Alliata 1952, p. 105; Troelsen 1954, p. 465), its appearance in the Anglo-Belgian basin is of particular interest. The distribution of *A. excentrica* and *A. gedgravensis* therefore will be examined in detail.

Distribution of Alliatina excentrica *and* Alliatinella gedgravensis *in the Gedgravian.* The Gedgravian deposits described in greatest detail in the literature are those of the Sutton outlier, near Woodbridge, Suffolk. These were 'zoned' by Prestwich (1871, pp. 116–20, text-figs. 1 and 2, pl. 6, maps and sections) and later discussed by Harmer in various papers (1898, pp. 320 et seq., text-figs. 5 and 6; 1902, p. 428, text-fig. 68; 1908, p. 92; &c.). Here the secondarily indurated 'Rock Bed' (Prestwich's 'Zone g'), the comminuted-shell sands ('Zone f'), and the top of the underlying marly sands ('Zone e') are all exposed, and the basal portion of the succession is easily attainable by hand auger. The Sutton deposits therefore were very thoroughly sampled, and since larger amounts of material were collected from here than elsewhere, the majority of the writer's specimens of *A. excentrica* and *A. gedgravensis* are from this locality.

One continuous section was obtained, consisting of a standing face, pit, and fruit-tree auger boring. The site was located in a small, now disused crag-pit, situated about 100 yds. west-north-west of a cottage on Occupation Road, and an equal distance north-east of Prestwich's Pit 'F' (Prestwich 1871, pl. 6, map). The succession is 28 ft. 3 in. thick, and rests on London Clay. It is materially the same as that seen in Pit 'F' (see Prestwich 1871, p. 119, text-fig. 2). The section was continuously sampled, each sample representing a stratigraphic interval of 6 in. The samples were numbered consecutively, from the top down.

In the first series of preparations covering the section, *A. excentrica* was found in seven samples—Nos. 18, 22, 23, 26, 31, 32, and 55 (see text-fig. 1). In Nos. 23, 26, and

[Palaeontology, Vol. 1, Part 1, 1957, pp. 76–86, pl. 14]



TEXT-FIG. 1. For explanation see text.

31 it is associated with *A. gedgravensis*. The latter species, unaccompanied by the former, was found in samples Nos. 9, 33, 34, 37, and 49. Since specimens of both species were found to be exceedingly rare (together constituting at most 0·5 per cent. of the assemblage in the 90–60-grain-size fraction) the distribution was checked by examination of additional material, processed from the same set of samples. Nos. 4, 9, 14, 19, 24, 29, 34, 39, 44, 49, and 54 were selected for the purpose. The lowest sample (No. 54) is from just above the base of the Gedgravian; the remainder are separated by 2-ft. intervals.

After washing, the preparations were thoroughly dried, sieved, and the foraminifera floated off the 90–60 fractions with carbon tetrachloride. All samples, except No. 4, which was too indurated to give satisfactory results, gave extremely rich foraminiferal concentrates (between 8,652 and 50,167 specimens per gramme of 90–60 fraction). *A. excentrica* was found in Nos. 9, 19, 24, 29, and 34, in all cases associated with *A. gedgravensis*. The latter, unaccompanied by the former, was found in Nos. 39, 44, and 49. Nos. 14 and 54 contained neither species. Details of relative abundance, &c., are given in text-fig. 1.

The distribution of the two species in the Sutton section is clearly defined. In the lower portion of the marly sands *A. excentrica* is almost absent, occurring only in sample No. 55. Above the junction between the marly sands and the comminuted-shell sand (the junction between Prestwich's 'Zones e' and 'f') it is sporadically distributed and rare. In the central part of the succession (the first 9 ft. below the junction), however, it is present, in relative abundance, in all of the eighteen samples. The distribution of *A. gedgravensis* is closely similar, although this species is more widely distributed throughout the lower portion of the marly sands than *A. excentrica*, and slightly less abundant than the latter in the central part of the section.

A lithological sequence resembling that at Sutton can be demonstrated in the much larger outlier of Orford at Richmond Farm, three-quarters of a mile south-west of the town (Harmer's Locality 9, see Harmer 1898, text-fig. 4). Here the exposed part of the Gedgravian consists of some 18 ft. of secondarily indurated, current bedded, comminuted-shell sand (Prestwich's 'Zone g'), which stands in vertical faces forming the walls of the farm stockyard. Augering at the base of one standing face has shown that the induration decreases rapidly downwards, and disappears about 5 ft. below the stockyard floor. Then, 11 ft. 8 in. below the floor, the unconsolidated comminuted-shell sands quite suddenly give place to soft, marly sands. The latter contain thin, impersistent seams of shells, and continue to the bottom of the hole at 25 ft. 6 in. below the floor. At this level caving occurred, and the hole was abandoned.

In this section the same method of sampling and numbering was used as at Sutton. *A. excentrica* and/or *A. gedgravensis* were found in samples Nos. 25, 46, 56, 60, 61, 62, 64, 65, 67, 69, 70, 73, 74, and 84. The majority of these samples are from the first 6 ft. below the comminuted-shell sand–marly sand boundary. Since no carbon tetrachloride separations were used, and the total number of specimens of the two species is not more than four in any one preparation, no reliable estimates of relative abundance can be made. Despite the limitations imposed by lack of concentrates, the distribution outlined above is clearly a reflection of that in the Sutton section. This is illustrated in text-fig. 1.

A. excentrica and *A. gedgravensis* have been found in materials from many of the classic exposures at the southern end of the Orford outcrop (Harmer's Locality 3, north of The Cliff, near Gedgrave; 6 and 7, Gedgrave Hall; and 12, Sudbourne Park). Their relative abundance in the assemblages is in harmony with that at Sutton. Both species have also been found in materials from the Tattingstone outlier south of Ipswich, but their distribution in this section has not been worked out in detail.

The occurrence at maximum abundance in a correlatable band in the Sutton and Orford outcrops suggests that the lithological break (the boundary between Prestwich's 'Zones e' and 'f') immediately overlying it has some stratigraphical significance. This belief is reinforced when the distribution of the other foraminiferal species is considered. Although the differences between the assemblages above and below the break are largely quantitative, and are to some extent governed by current sorting (Carter 1951), they are constant, and can be recognized in all three of the Gedgravian outliers (Tattingstone, Sutton, and Orford–Aldeburgh). In a later paper the foraminiferal faunas as a whole will be discussed, and evidence will be produced favouring a subdivision of the Gedgravian into two, an upper portion correlated with the Scaldisian of the Low Countries, and a lower portion correlated with the Upper Diestian.

The occurrence of Alliatina excentrica *in the Upper Diestian and Scaldisian of Belgium.* In connexion with another matter the writer had occasion to examine the Casterlian and Scaldisian materials from the Kattendyk Dock excavations, Antwerp, in the Burrows and Holland Collection at the British Museum (Natural History), London (see Burrows and Holland 1897, p. 393). The specimen of '*Pulvinulina auricula* (Fichtel and Moll)' recorded from the Scaldisian (Burrows and Holland 1897, p. 391, no. 363) turned out to be *A. excentrica* (found in cell 32 of an uncatalogued slide labelled 'Scaldisian Inf. Kattendyk Docks, Antwerp, 'A').

Although *A. excentrica* was not recorded by van Voorthuysen and Pannehoek (1951), it is sparingly present in the base of the Upper Diestian in the Kruisschans Boring, near Antwerp. Two broken specimens were found by the writer in sample No. 6.

Alliatinella gedgravensis has not been recorded from the Low Countries, nor has it been found in materials available to the writer. Its constant association with *A. excentrica* in the Gedgravian indicates that it is probably present but exceedingly rare, and has so far escaped notice by Belgian and Dutch workers.

The occurrence of Alliatina excentrica *and* Alliatinella gedgravensis *in the Pliocene of Italy*. The types of *A. excentrica* are from the Upper Pliocene 'Astian' of Castel Arquato (Piacenza), northern Italy (Napoli Alliata 1952, p. 106). Additional specimens were recorded by Troelsen (1954, p. 465) from the Upper Pliocene of Valle Andona, northern Italy. The species is also present in Burrows and Holland's material from the 'Plaisancian' of Bordighera, Italy (in cell 14 of an uncatalogued slide labelled 'Bordighera Pliocene "B"'). It was placed by them in *Nonionina scapha* (Fichtel and Moll) (Burrows and Holland 1897, p. 390, no. 385).

Although *A. gedgravensis* has not been recorded from the Italian Pliocene it is present in the Upper Pliocene 'Astian' of Valle Andona, northern Italy. One specimen has been found in materials from that locality in the Imperial College Collections. It is associated with *A. excentrica.*

The distribution of the genus Alliatina *in Recent seas*. Examination of Millett's figured specimen of *Bulimina convoluta* Williamson var. *nitida* (1900, p. 280, pl. 2, figs. 10*a–c*) from the Malay Archipelago has confirmed Troelsen's suspicion that the species should be placed in the genus *Alliatina* (Troelsen 1954, p. 465). Millett's specimen is identical with the type figures of Cushman and McCulloch's '*Cushmanella primitiva*' (1940, pl. 18, figs. 6–10). These workers appear to have overlooked the assymetrical form of the supplementary aperture and 'internal tube', and '*Cushmanella primitiva*' should be placed in synonymy with *Alliatina nitida* (Millett). The types of the former are from

Darwin's Bay, Tower Island, in the Galapagos Group, at 17 fathoms. The range is given as Braithwaite Bay, Socorro Island, Mexico, in 4–10 fathoms, southward to Port Utria, Colombia, in 20 fathoms, with records from points between at depths varying between 4 and 80 fathoms.

'*Bulimina convoluta* var. *nitida*' was recorded by Sidebottom (1905, p. 13) from Delos in the Grecian Archipelago, and by Heron-Allen and Earland (1915, p. 642) from the Kerimba Archipelago, East Africa. The figured specimen from Delos belongs to a species of *Alliatina*, as do the majority of the specimens recorded from the Kerimba Archipelago. This is widely distributed in the latter area, and is usually associated with a species of *Pseudobulimina*, as in the Malay Archipelago. It occurs in materials from Stations Nos. 1, 3–6, 9, 11, and 12, at depths ranging from 5 to 18 fathoms. Heron-Allen and Earland's specimens of '*B. convoluta*' from Station 11 also belong in *Alliatina*.

The genus *Alliatina* is also represented in Heron-Allen and Earland's materials from 16 fathoms, Friendly Islands (Tonga Group), '*B. convoluta* Williamson' (with a species of *Pseudobulimina*); Delos (ex Millett's Colln.) '*B. convoluta* var. *nitida*' (with *Cushmanella browni* (d'Orbigny)); and Sulu Roadstead, '*B. convoluta* var. *nitida*'. Their specimens of *B. convoluta* var. *nitida* from Port Darwin, Australia, however, should be placed in *C. brownii*.

The significance of the distribution of Alliatina excentrica *in the Pliocene of Italy and the Anglo-Belgian basin*. Although the records of *Alliatina* in Recent seas are few, they clearly indicate that the genus characteristically inhabits shallow tropical waters. Its absence from the shallow-water assemblages of the Atlantic and North Sea coasts of Europe is a consequence of the relatively low temperatures prevailing in these areas. The occurrence of this genus in the Pliocene of the Anglo-Belgian basin suggests the existence at that time of a climate considerably warmer than that now prevailing. This hypothesis is in harmony with the evidence provided by the molluscs and the polyzoa. The rarity of *A. excentrica* in the Pliocene assemblages of the Anglo-Belgian basin probably indicates that this area was very near the northern limit of distribution of the species.

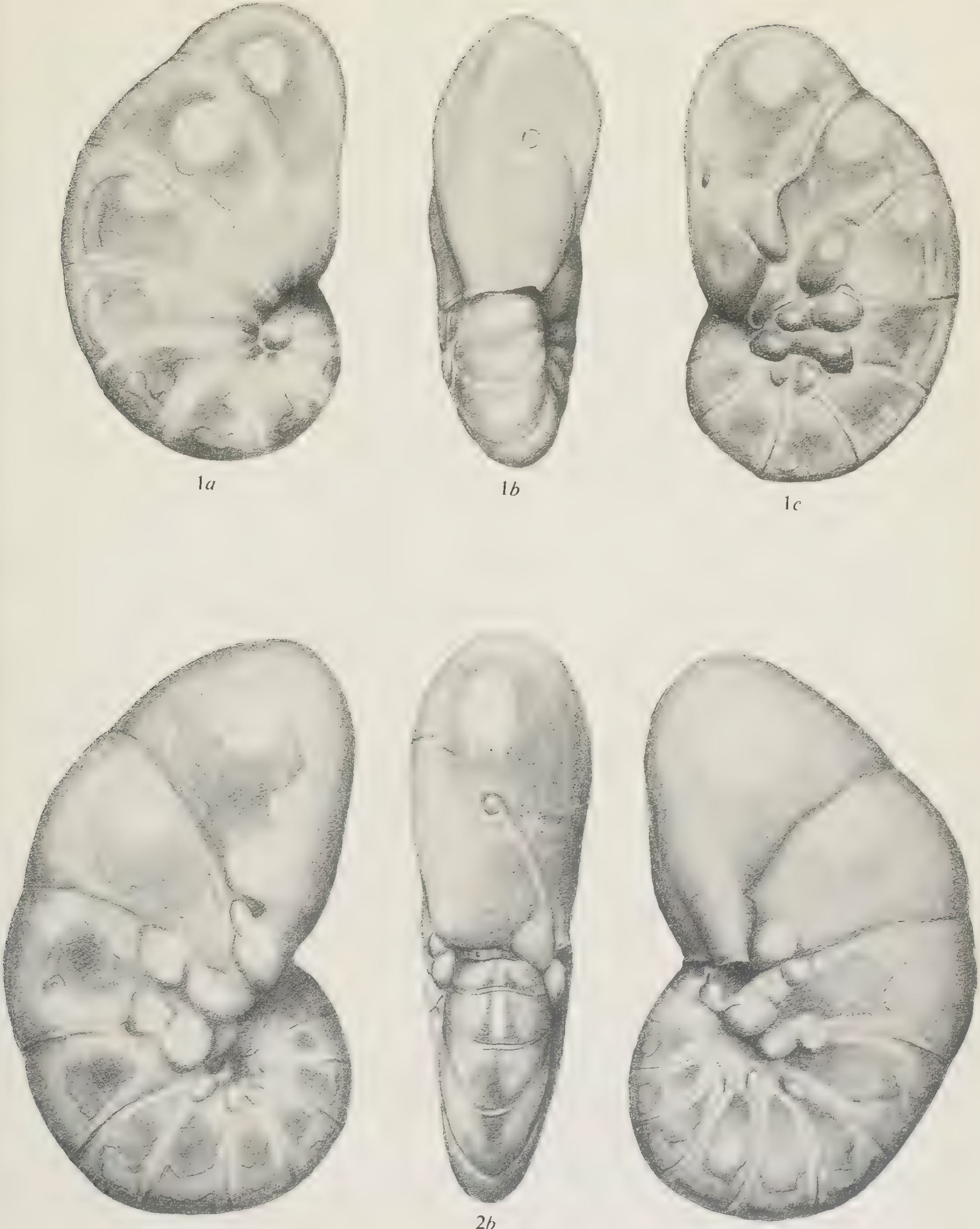
The Plio-Pleistocene boundary in the Anglo-Belgian basin is usually taken where evidence of climatic deterioration first becomes manifest with the first appearance of typically arctic species of *Elphidiella* ('*E.* cf. *arctica* (Parker and Jones)' of van Voorthuysen, = '*E. arctica* (Parker and Jones)' of Lagaaij = *E. hannai* (Cushman and Grant); see Lagaaij 1952, p. 203). In East Anglia this is at the base of the Waltonian Red Crag (see van Voorthuysen and Pannekoek 1951, diag. no. 2), and it is precisely here that *A. excentrica* disappears. In view of the similarity between the Plio-Pleistocene faunal sequences on the two sides of the North Sea basin it seems likely that *A. excentrica* will prove to have a similar distribution in the Low Countries, and will serve as a useful climatic-stratigraphic marker.

EXPLANATION OF PLATE 14

Figs. 1*a–c*. *Alliatinella gedgravensis* gen. et sp. nov. Holotype, Brit. Mus. Cat. No. P. 43459. 1*a*, dorsal view; 1*b*, apertural view; 1*c*, ventral view. ×183.

Figs. 2*a–c*. *Alliatina excentrica* (di Napoli Alliata). Hypotype, Brit. Mus. Cat. No. P. 43462. 1*a*, dorsal view; 1*b*, apertural view; 1*c*, ventral view. ×183.

PLATE 14



1*a* 1*b* 1*c*

2*a* 2*b* 2*c*

CARTER, Pliocene *Foraminifera*

Since *Alliatinella gedgravensis* has not been found in Recent material no direct evidence concerning ecologic factors governing its distribution is available. Since its distribution in the Gedgravian resembles that of *A. excentrica* it is likely that it also is a shallow, warm-water species. Its absence from the post-Gedgravian deposits in eastern England supports this belief. If the non-appearance of this species in Recent seas is real, and not due to collection failure, it must become extinct at some level in the Pleistocene or Holocene. Its total time-range cannot be worked out until more information is available concerning post-Pliocene faunal successions in areas far enough south to be relatively little affected by the Pleistocene refrigeration.

Acknowledgements. The writer wishes to thank Drs. R. H. Hedley and C. G. Adams of the British Museum (Natural History), London, and Dr. F. W. Anderson of the Geological Survey and Museum, London, for facilitating access to type collections in their charge, and Dr. J. H. van Voorthuysen for splits of samples from the Kruisschans Boring, near Antwerp, and gifts of other Plio-Pleistocene materials from the Low Countries.

SYSTEMATIC PALAEONTOLOGY

Family CERATOBULIMINIDAE Glaessner (emend. Troelsen)

Genus ALLIATINA Troelsen

Type species *Cushmanella excentrica* di Napoli Alliata

Alliatina excentrica (di Napoli Alliata)

Plate 14, figs. 2*a–c*

Pulvinulina auricula (Fichtel and Moll), Burrows and Holland 1897, pp. 390–1, no. 363 (part).
Nonionina scapha (Fichtel and Moll), Burrows and Holland 1897, pp. 390–1, no. 385 (part).
Cushmanella excentrica di Napoli Alliata 1952, pp. 11–13, pl. 5, figs. 1, 1*a*, 1*b*.
Alliatina excentrica (di Napoli Alliata), Troelsen 1954, p. 465, pl. 11, figs. 4–6, 8, 9, 12.

Remarks. The Gedgravian specimens agree in most respects with those very fully described and illustrated by Troelsen (1954). In the majority, however, the supplementary aperture is closed by a very thin calcareous plate, and is non-functional. When a new chamber is added this plate is resorbed, and the resulting perforation functions as a septal foramen. The plate is very fragile, and is often broken in fossil specimens. Adult individuals of the species attain a maximum larger diameter of 0·50 mm.

Distribution. Upper and Lower Gedgravian (Pliocene) of eastern England; Upper Pliocene 'Astian', Pliocene 'Plaisancian' of northern Italy; Pliocene Upper Diestian and Scaldisian of Belgium.

Dimensions of figured specimen. Hypotype; larger diameter 0·45 mm., smaller diameter 0·28 mm., thickness 0·15 mm.

Horizon and locality. Figured hypotype; carbon tetrachloride flotation, sample no. L22/1, base of Upper Gedgravian comminuted-shell sands, about 2 ft. above its junction with the Lower Gedgravian marly sands, Harmer's Locality 7 (see Harmer 1898, fig. 4) in disused crag-pit adjacent to Lower House Cottages, Gedgrave Hall, 1¼ miles south-west of Orford, Suffolk, England.

Repository. Figured hypotype (Brit. Mus. Cat. No. P. 43462), Dept. of Foraminifera, British Museum (Natural History), London; unfigured hypotypes (Foram. Research Cat. Nos. 150/1–8, 151/1–21, 152/1–37, 153–62), Dept. of Geology, Imperial College, London.

Genus ALLIATINELLA gen. nov.

Type species *Alliatinella gedgravensis* sp. nov.

Diagnosis. Lateral outline, wall structure, shape of chambers, position and shape of basal aperture, shape and orientation of internal partition, and direction of coiling identical in all respects with that of *Alliatina*, but coiling distinctly and consistently trochospiral, accessory chambers developed only on the ventral side, and supplementary aperture offset towards the ventral side of the apertural face. In ventral view the genus is scarcely distinguishable from *Alliatina*, from the dorsal side it shows a surprising and quite misleading resemblance to a juvenile *Cancris*. In apertural view the genus is markedly asymmetrical.

Relationships. In his paper on the Ceratobuliminidae Troelsen (1954, p. 464) discusses the relationship between the genera *Alliatina* and *Cushmanella*. Under 'Remarks' he states—'Palmer and Bermudez's figures (1936) of *Cushmanella brownii* (d'Orb.), the genotype of *Cushmanella*, are not particularly clear, but in their diagnosis they expressly state that the test is bilaterally symmetrical. Hofker (1951, fig. 11*a*) represents the internal tube in *C. brownii* as being bilaterally symmetrical and entirely different in its construction from the internal partition of *Alliatina*', and in 'Postscript 3'—'The assumption of a fundamental difference between *Cushmanella* and *Alliatina* is confirmed through examination of topotypes of *C. brownii* (D'Orb.) . . .' (the word 'fundamental' is deleted in the separate kindly sent to the writer by Dr. Troelsen). The writer is unable to agree with the views expressed by Dr. Troelsen. *Cushmanella* is considered to be closely related to *Alliatina*, and both to *Alliatinella*.

The differences between *Cushmanella*, *Alliatina*, and *Alliatinella* are fundamentally those of symmetry. Examination of specimens of *C. brownii* in the Heron-Allen and Earland Collection in the British Museum has shown that the 'internal tube' is identical with the inverted-V-shaped internal partition of the other two genera, except that it is symmetrically orientated relative to the plane of coiling, and free on both margins ('dorsal' and 'ventral' margins by homology with *Alliatina* and *Alliatinella*). The supplementary aperture (Hofker's 'Protoforamen', 1951, fig. 11*a*) is arranged parallel to the basal suture (not obliquely, as in the other two genera), and is hour-glass shaped, but these features are controlled by the position of the internal partition, and the curling under of its free margins. *C. brownii* is otherwise identical with the type species of *Alliatina*.

The relationship between *Alliatina* and *Alliatinella* is self-evident. The differences between the two genera are similar in essence to those between *Cushmanella* and *Alliatina*.

Alliatinella, *Alliatina*, and *Cushmanella* constitute a morphological series in increasing bilateral symmetry. If Palmer and Bermudez's record of *Cushmanella* from the Late Tertiary of Cuba refers to an *Alliatina*, as is likely, the writer's belief that this series is evolutionary would be very strongly supported by the geological ranges—*Alliatinella*, Pliocene; *Alliatina*, Pliocene and Recent; *Cushmanella*, Recent.

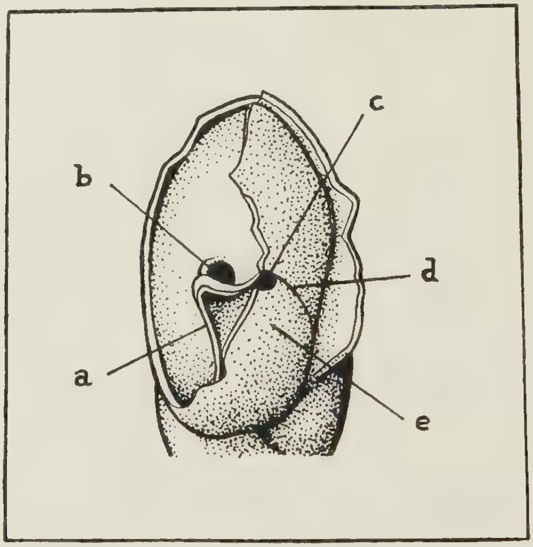
The internal partition of *Alliatinella* is very similar in form to that of *Ceratobulimina*, and the two genera have identical wall structure and constant dextral coiling. According to Troelsen (1954, pp. 450, 453, 464) the septal foramen in the type species of *Ceratobulimina* is secondary. Hofker (1954, p. 147), however, states it to be homologous with the distal portion of the apertural foramen (supplementary aperture) of the previous chamber. In *Alliatina*, *Alliatinella*, and *Cushmanella* the supplementary aperture is apparently non-functional, and is closed by a thin plate. When a new chamber is formed the plate is resorbed, and the perforation produced functions as the septal foramen. Until this anomaly is explained the systematic position of the three latter genera must remain doubtful. They are tentatively placed in the Ceratobuliminidae.

Alliatinella gedgravensis sp. nov.

Plate 14, figs. 1*a–c*; text-fig. 2

Cristellaria gibba (d'Orbigny), Jones 1895, pl. 7, figs. 19*a*, *b*.
Cristellaria gibba (d'Orbigny), Jones 1896, pp. 247–8 (part).
Cristellaria gibba (d'Orbigny), Burrows and Holland 1897, pp. 384–5, No. 233 (part).

Description. Test free, ear shaped in lateral view, with broadly rounded periphery, coiled in a low, dextral trochospiral. Chambers of two kinds: large conspicuous primary chambers, scarcely if at all inflated, and small blister-like accessory chambers arranged in two or three series, covering the sutures between the primary chambers near the umbilical margin on the ventral side, usually not developed on the suture between the ultimate and penultimate primary chambers. Sutures distinct, white, slightly depressed in the later growth stages. Apertures of two kinds: one a simple slit at the base of the apertural face, the other non-functional, an oblique oval in the apertural face, slightly offset towards the ventral side, sealed with a very thin, calcareous plate. Internal partition (see 'a', text-fig. 2) asymmetrical and inverted-V-shaped in cross-section, extending obliquely across the primary chamber, formed by a completely enclosed invagination of the ventral chamber wall. Anterior attachment of partition to inside of apertural face, marked externally by a groove (see 'd', text-fig. 2) extending obliquely from the ventral umbilicus to the top of the non-functional aperture, which is enclosed above, on the dorsal (spiral) side, and below by a fold in the partition; dorsal (spiral) margin of the partition free, running posteriorly from beneath the non-functional aperture to the base of the previously formed apertural face (septum) near the spiral suture; posterior margin joined to previously formed apertural face (septum), running from the spiral suture to the base of the septal foramen (see 'b', text-fig. 2) formed by resorbtion of the plate covering the previous supplementary aperture, then turning sharply down to the ventral umbilicus. Chamber walls calcareous, finely perforate, layered, with a glistening surface, outer layers thin or missing in two narrow bands running round the test, one on either side of the periphery, occasionally over the whole of the lateral surfaces of the chambers. Pores radially arranged, occasionally enlarged, and passing right through the test wall; enlarged pores more abundant where the outer layers of wall material are thin or missing. Maximum larger diameter of adult specimens up to 0·48 mm.



Text-fig. 2. *Alliatinella gedgravensis* gen. and sp. nov. Paratype, Brit. Mus. Cat. No. P. 43460. Apertural view of dissection illustrating relationship of internal partition to septal foramen. *a*, internal partition; *b*, penultimate septal foramen; *c*, ultimate septal foramen; *d*, groove on anterior surface of ultimate septum, marking line of attachment of ultimate internal partition; *e*, ultimate septum (apertural face of penultimate chamber). ×183.

Remarks. The first reference to this species was by Jones (1895), who misidentified it with *Cristellaria gibba* d'Orbigny. Two figures of a Gedgravian specimen from Sutton were given (figs. 19*a* and *b* on pl. 7), one showing it in side view (fig. 19*a*), the other in apertural view. The latter shows the coiling to be planospiral. Examination of the original specimen in the Burrows Collection at the Geological Survey and Museum, London (Cat. No. Mik(T) 101001), shows that this drawing is inaccurate, and that the specimen should be placed in the species here designated *Alliatinella gedgravensis*. The illustrations for pl. 7, which were executed by either Burrows or Holland (see footnote, under plate explanation, Jones 1895), are all very formalized, and most of them are obviously based on several specimens. Fig. 19*a* is a fair representation of the dorsal view of the original, but fig. 19*b* probably illustrates a misinterpreted apertural view of *Alliatina excentrica*. It seems likely that Jones based his identifications on the figures rather than the specimen, for in his description (1896) he states—'This small subovate form is one of the many intermediate to the closely coiled *Cristellaria rotulata* and the more expanded and elongate *C. crepidula*. It has many cogeners, varying in relative thickness and other unimportant features.' Further comment is unnecessary.

In 1897 Burrows and Holland added a record of '*C. gibba*' from 'Zone g' (see Prestwich 1871, p. 121) of Gedgrave, near Orford. If the specimens so recorded are present in their collections from that locality they resemble neither the figured specimen nor the figures of it on pl. 7.

Distribution. Upper and Lower Gedgravian (Pliocene) of eastern England; Upper Pliocene 'Astian' of northern Italy.

Horizon and locality. Holotype, figured and unfigured paratypes; carbon tetrachloride flotation, sample no. L22/1, base of Upper Gedgravian comminuted-shell sands, about 2 ft. above its junction with the Lower Gedgravian marly sands, Harmer's Locality 7 (see Harmer 1898, fig. 4) in disused crag-pit adjacent to Lower House Cottages, Gedgrave Hall, 1¼ miles south-west of Orford, Suffolk, England.

Dimensions of figured specimens. Holotype; larger diameter 0·36 mm., smaller diameter 0·22 mm., thickness 0·13 mm.; dissected paratype; larger diameter 0·43 mm., smaller diameter 0·21 mm., thickness 0·13 mm.

Repository. Figured holotype (Brit. Mus. Cat. No. P. 43459), Dept. of Foraminifera, British Museum (Natural History), London; figured dissected paratype (Brit. Mus. Cat. No. P. 43460), ibid.; unfigured paratypes (Brit. Mus. Cat. No. P. 43461), ibid. (Foram. Research Cat. Nos. 163, 164), Dept. of Geology, Imperial College, London.

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